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Two New Species of *Pseudoyelicones* (Braconidae: Rogadinae) from Costa Rica

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Abstract.—Two new species of the braconid wasp genus *Pseudoyelicones* van Achterberg, Penteado-Dias and Quicke from Costa Rica are described and illustrated, ***P. limonensis* sp.n.** and ***P. rojasi* sp.n.**, bringing the total number of species of *Pseudoyelicones* known to five, four of which are recorded from Costa Rica. Additionally, six more specimens of *P. nigriscutum* van Achterberg and Quicke are recorded. A modification to the key of van Achterberg, Penteado-Dias and Quicke (1997: Zoologische Mededeelingen. Leiden 71: 1–8) is included to differentiate *P. limonensis* sp.n. and *P. rojasi* sp.n. from similar species.

Key words.—Braconidae, Rogadinae, *Pseudoyelicones*, *Yelicones*, new species.

van Achterberg, Penteado-Dias and Quicke (1997) described the genus *Pseudoyelicones* to accommodate three highly aberrant species of rogadine parasitic wasps from Brazil and Costa Rica. *Pseudoyelicones* species superficially look very similar to those of a highly distinctly braconid wasp genus *Yelicones* Cameron in that they are robust wasps with swollen femora, shortened medial tarsal segments, laterally compressed hind basitarsus, a strongly slanted labrum, and have a large triangular basal area on the second metasomal tergite (van Achterberg, Penteado-Dias and Quicke 1997). However it can be distinguished easily from *Yelicones* by the strongly curved hind wing vein SR which lies within a highly corrugated area of the wing membrane. In addition, its mandible is distinctly bidentate rather than tridentate, the precoxal suture and occipital carina are absent, the tarsal claws are not pectinate, the telotarsi hardly or not enlarged, fore wing vein M+CU is straight apically, hind wing vein 1r-m is vertical, vein 2-SC+R is vertical and widened and vein m-cu is very short or indistinct.

Yelicones is cosmopolitan and available host records suggest that they are solitary endoparasitoids of various pyralid moth larvae (Quicke and Kruft 1995; Areekul and Quicke submitted). In contrast, *Pseudoyelicones* is known only from the Neotropical region to date. Its biology is unknown, although all Rogadinae *sensu stricto* (ie. Rogadini of many authors) are koinobiont endoparasitoids of Lepidoptera larvae whose remains they mummify before pupating within the host (Shaw and Huddleston 1991). The large eyes and ocelli of *Pseudoyelicones* species, and their yellow or brownish yellow colour, suggest that they are probably nocturnal, as are many *Yelicones* species and most other Rogadinae (Gauld and Huddleston 1976; Quicke, Austin and Chishti 1998).

Here we describe two new species discovered recently in the collection of INBio, Costa Rica, originally misidentified as *Yelicones* species. Although all known species

of *Pseudoyelicones* are morphologically very similar, the new species indicate that some details of sculpture may be of taxonomic use in the genus, in addition to colour and size. Six additional specimens of *P. nigriscutum* van Achterberg were located in the INBio collection, all from the same locality, Province Punta, as the holotype.

MATERIALS AND TERMINOLOGY

Material was sorted from the collection of the Instituto Nacional de Bioversidad (INBio), Santo Domingo de Heredia, Costa Rica. A middle leg from one side of the body was removed from a paratype specimen of *P. limonensis* sp.n. and *P. nigriscutum* for DNA sequencing. The specimens were then photographed using Automontage®. Terminology largely follows that of van Achterberg (1979, 1988). Description of sculpture follows Harris (1979).

SYSTEMATICS

Genus *Pseudoyelicones* van Achterberg, Penteado-Dias and Quicke, 1997
Type species, *Pseudoyelicones manoeli* van Achterberg and Penteado-Dias by original designation.

DESCRIPTIONS

Pseudoyelicones limonensis sp.n.
(Figs 1–6)

Material.—Holotype female, "Cerro Tortuguero, P.N. Tortuguero, 0–100m. Prov. Limon, COSTA RICA. J. Solano, Mar 1991. L_N-285000, 588000", "COSTA RICA INBIO CRI000 317905" (INBC). Paratype, female, "Amubri 70m, Talamanca Prov. Limon, Costa Rica, 12 a 30 set. 1992. G. Gallardo L_S 385500, 578050", "COSTA RICA INBIO CRI000 960331" (INBC).
Holotype, length of body 8.5 mm, of fore wing 7.0 mm.

Head.—Antennae with 52 flagellomeres; terminal flagellomere acuminate, approximately 3.0 times longer than wide; length of third flagellomere as long as fourth; length of third, fourth and penultimal flagellomeres 0.6, 0.6 and 1.7 times their widths, respectively; malar space with moderately dense, long setosity; height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.3:4.8:1.0; face transversely carinate with sparse long setosity (Figs. 1, 2); height of eye: width of face: width of head = 1.6:1.0:2.3; width of hypoclypeal depression 0.5 times minimal width of face; length of malar space 0.4 times basal width of mandible; eye glabrous; length of eye in dorsal view 2.6 times temple (Fig. 3); occiput and temple smooth; post-ocellar length: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0:2.0:1.0.

Mesosoma.—Smooth, moderately densely setose, 1.6 times longer than high; mesoscutum distinctly higher than pronotum anteriorly; notauli deep, weakly crenulated, impressed on anterior half of mesoscutum; scutellus sulcus with 3 carinae between the two outer ones; median area of metanotum keel; scutellum largely smooth, weakly striate posteriorly, postero-medially with distinct carina; mesopleuron shiny and smooth (Fig. 4); propodeum with distinct median carina, finely granulate, posterior half transversely carinate (Fig. 5).

Wings.—Fore wing: lengths of veins SR1: 3-SR: r = 1.0:4.8:2.5; vein 1-SR+M straight; vein r arising 0.5 distance from base of pterostigma; lengths of veins 2-SR: 3-SR: r-m = 1.1:1.9:1.0; lengths of veins 2-SR+m: 2-M: m-cu = 1.0:2.3:1.0; lengths of veins 2-CU1: 1-CU1 = 4.0:1.0; lengths of veins 2-CU1: 3-CU1 = 4.0:1.0; veins C+SC+R and 1-SR forming an angle of 45°. Hind wing: vein cu-a unsclerotised; vein m-cu indistinct; basal cell, subbasal cell and basal parts of marginal and submarginal cells glabrous (Fig. 6).

Legs.—Lengths of fore femur: tibia: tarsus = 1.1:1.3:1.0; length of fore femur 2.3 times longer than deep; fore tibia with distinct longitudinal ridge; hind femur 2.3

times longer than deep; lengths of hind femur: tibia: basitarsus = 1.7:2.3:1.0; hind basitarsus 3.1 times longer than deep; length of hind tibial spurs 0.5 and 0.6 times hind basitarsus.

Metasoma.—Shiny and sparsely setose; first tergite with anterior 0.6 weakly striate, dorsal carinae uniting before the level of spiracles, with distinct, nearly complete median carina; second tergite smooth, antero-medially with smooth triangular area produced posteriorly to form incomplete medial carina; second suture smooth, indistinct; tergites 3–7 smooth; length of ovipositor sheath 0.05 times fore wing.

Colour.—Yellow; antennae basally brownish yellow with apical 17 flagellomeres somewhat darker brown; stemmaticum dark brown; ovipositor sheath brown; wing membrane very pale yellow; wing veins brownish yellow except veins apical 0.7 of 1SR+M, m+cu, 3-CU1 and CU1a, brown.

Etymology.—Named after type locality, Limon Province.

Comments.—This species is similar to *P. manoeli* van Achterberg and Penteado Dias but can be easily separated by the apical segment of the antennae which is brown rather than ivory and by the propodeum which has distinct transverse carinae posteriorly (Fig. 5).

Pseudoyelicones rojasi sp.n.
(Figures 7–12)

Material.—Holotype, female, "Sector Cerro Cocori, Fca. De E. Rojas, 150m, Prov. Limon, Costa Rica, E. Rojas, 28 may a 17 jun 1992, L-N 286000, 567500", "COSTA RICA INBIO CRI000 764364" (INBC). Holotype, length of body 7.0 mm, of fore wing 5.0 mm.

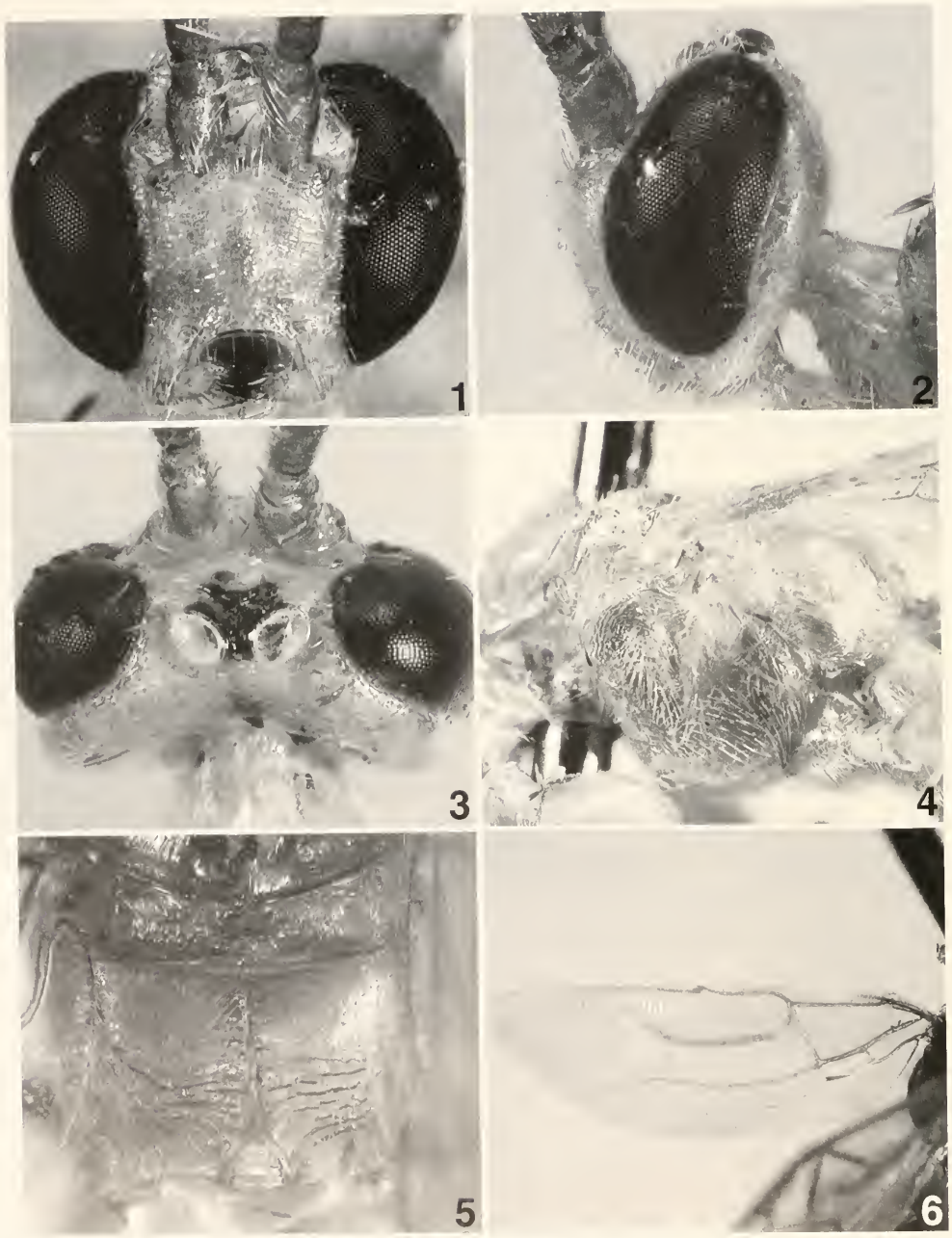
Head.—Antennae with 42 flagellomeres; terminal flagellomere acuminate, approximately 2.5 times longer than wide; third flagellomere 1.1 times length of fourth; length of third, fourth and penultimate flagellomeres 0.9, 0.9 and 1.6 times their widths, respectively; malar space moderately long setose; height of clypeus: intertentorial distance: tentorio-ocular distance = 1.3:4.4:1.0; face transversely carinate with moderately sparse long setosity (Fig. 7); height of eye: width of face: width of head = 1.4:1.0:2.2; width of hypoclypeal depression 0.5 times minimal width of face; length of malar space 0.5 times basal width of mandible; eye glabrous; length of eye in dorsal view 3.1 times temple (Fig. 8); occiput and temple smooth; post-ocellar length: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0:2.5:1.0.

Mesosoma.—Smooth, shiny, moderately densely setose, 1.8 times longer than high; mesoscutum distinctly higher than pronotum anteriorly, postero-medially coarsely striate; notauli deep, smooth, impressed on anterior half of mesoscutum; scutellus sulcus with 5 carinae between the two outer ones; medial area of metanotum with keel; scutellum completely finely longitudinally striate (Fig. 9), postero-medially with distinct carina; mesopleuron largely smooth (Fig. 10); propodeum with distinct median carina, finely granulate anteriorly, with weak, irregular transverse carinae posteriorly (Fig. 11).

Wings.—Fore wing: lengths of veins SR1: 3-SR: r = 1.0:8.4:4.4; vein 1-SR+M straight; vein r arising half way along pterostigma; lengths of veins 2-SR: 3-SR: r-m = 1.0:1.9:1.1; lengths of veins 2-SR+M: 2-M: m-cu = 1.0:4.0:1.5; lengths of veins 2-CU1: 1-CU1 = 4.0:1.0; lengths of vein 2-CU1: 3-CU1 = 2.5:1.0; veins C+SC+R and 1-SR forming an angle of 30°. Hind wing: both destroyed.

Legs.—Lengths of fore femur: tibia: tarsus = 1.4:1.7:1.0; length of fore femur 2.4 times longer than deep; fore tibia with distinct longitudinal ridge; hind femur 2.4 times longer than deep; lengths of hind femur: tibia: hind basitarsus = 1.5:1.9:1.0; hind basitarsus 4.0 times longer than deep; length of hind tibial spurs 0.4 and 0.5 times hind basitarsus.

Metasoma.—Moderately sparsely setose;



Figs. 1–6. *P. limonensis* sp.n. 1, frontal view of face; 2, lateral view of head; 3, dorsal view of head; 4, lateral view of mesosoma; 5, dorsal view of propodeum; 6, hind wing.

anterior 0.6 of first tergite weakly striate, 1.2 times wider than medially long, dorsal carinae uniting before the level of spiracles, with distinct, nearly complete medial carina (Fig. 12); second tergite largely smooth, 1.9 times wider than medially long, antero-medially with smooth triangular area produced posteriorly to form

incomplete medial carina (Fig. 12); second suture distinct laterally, indistinct medially, smooth; third tergite smooth, 2.4 times wider than medially long; tergites 4–7 smooth; length of ovipositor sheath 0.06 times fore wing.

Colour.—Largely pale yellow; antennae basally yellow, distally 10 flagellomeres brown except apical flagellomere very pale yellow; head, metasomal tergites 1–3, brownish yellow; stemmaticum, tegula, scutellum except disc, metanotum, pterostigma, legs, apical 0.2, 0.3 and 0.3 of fore, mid and hind femora, fore, mid and hind tibiae, dark brown; metasomal tergites 4–7, mesopleuron antero-dorsally, ovipositor sheath and ovipositor, brown; wings veins yellow except for veins 1-SR+M, 2-CU1, 3-CU1, m-cu and CU1a brownish yellow, membrane very pale yellow except for first discal cell entirely and second discal cell basally, very pale brown.

Etymology.—Named after its collector.

Comments.—This is a distinctive species because of its scutellum which is completely striate (Fig. 9).

KEY TO *PSEUDOYELICONES* SPECIES

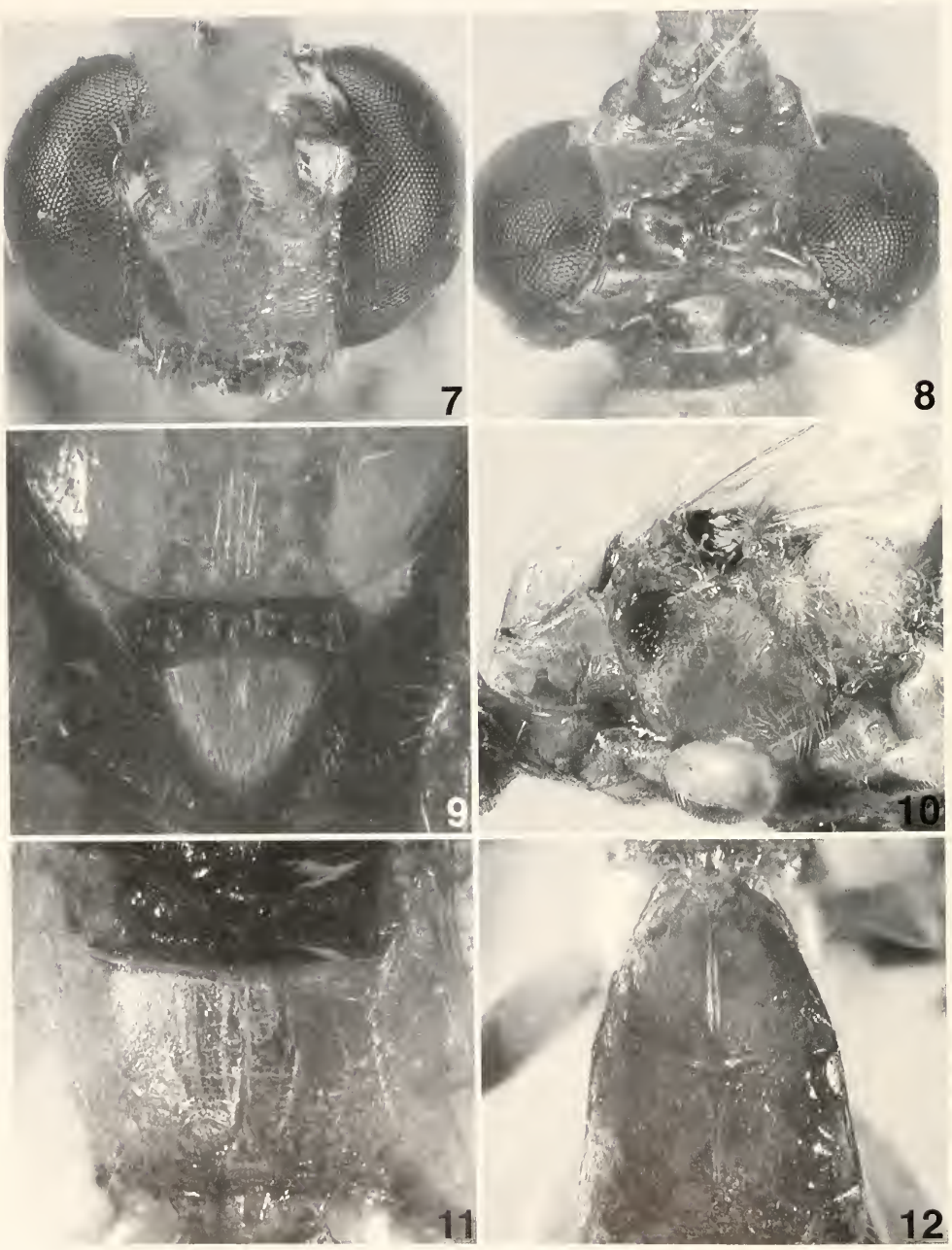
The following is a modified version of the key to *Pseudoyelicones* species by van Achterberg, Penteado-Dias and Quicke (1997) accommodating the new species described here.

1. Mesoscutum and scutellum completely black or dark brown; apex of hind tibia yellow, contrasting with dark brown remainder of tibia; area below pterostigma distinctly darkened and contrasting with sub-hyaline apex of fore wing ..... ***P. nigriscutum* van Achterberg**
– Mesoscutum and scutellum not as above (Fig. 9); colour of apex of hind tibia not as above; area below pterostigma slightly darkened and not or hardly contrasting with apex of fore wing 2

2(1) Pterostigma (except narrowly at base and at apex), mesopleuron antero-dorsally, middle and hind tibiae and apices of femora dark brown (Fig. 10); length of fore wing 3–5 mm 3
– Pterostigma, mesopleuron antero-dorsally, middle and hind tibiae and apices of femora brownish-yellow (Fig. 4); length of fore wing about 8 mm 4

3(2) Scutellum distinctly finely striate (Fig. 9); mesoscutum postero-medially with large area of finely striae (Fig. 9); mesoscutum completely yellow; scutellum yellow except posteriorly dark brown (Fig. 9); basal 3 metasomal tergites completely brown (Fig. 12); fore wing vein 1-CU1 yellow ..... ***P. rojasi* sp.n.**
– Scutellum smooth, without striae; mesoscutum postero-medially with narrow area of fine striae; mesoscutum brownish yellow except laterally dark brown; scutellum dark brown except for medially paler; 1st and 2nd metasomal tergites brownish yellow except for first tergite postero-medially, second tergite medially and posteriorly dark brown, third tergite largely dark brown; fore wing vein 1-CU1 dark brown ..... ***P. phaeostigma* van Achterberg and Quicke**

4(2) Apical segment of antennae ivory; propodeum densely rugulose, without distinct transverse carinae posteriorly; wing veins brownish yellow except for veins r, 3-SR, 2-SR, 1-SR+M, 2-M, m-cu and 3M dark brown ..... ***P. manoeli* van Achterberg and Penteado-Dias**
– Apical segment of antennae brown; propodeum with microsculpture anteriorly, posteriorly with distinct transverse carinae (Fig. 5); wing veins yellow except fore wing veins 1-SR+M, m-cu, 3-CU1 and CU1a dark brown ..... ***P. limonensis* sp.n.**



Figs. 7–12. *P. rojasi* sp.n. 7, fronto-dorsal view of face; 8, dorsal view of head; 9, dorsal view of posterior part of mesoscutum and scutellum showing fine longitudinal striation of the latter; 10, lateral view of mesosoma; 11, dorsal view of propodeum; 12, dorsal view of first and second metasomal tergites.

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Species of Microdontomerini (Hymenoptera: Chalcidoidea: Torymidae) Associated with Galls of Cynipidae (Hymenoptera) in Europe

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Abstract.—A key is given to European species in the genera *Adontomerus* and *Idiomacromerus* that are parasitoids in galls of Cynipidae, and the known host associations of the eight species are reviewed. Two of the six species of *Idiomacromerus*, ***I. silybi*** **Askew** and ***I. urospermi*** **Askew**, are described as new, and characters separating *Idiomacromerus* and *Pseuderimerus* are discussed.

A number of species of *Adontomerus* Nikol'skaya and *Idiomacromerus* Crawford, related genera within the torymid tribe Microdontomerini (Grissell 1995; Askew 2000), have been reared from cynipid galls as parasitoids of the gall-formers or possibly of other chalcid parasitoids. It is mostly galls of Aylacinae developing on herbaceous plants that are attacked, chiefly in southern Europe, and in these galls Microdontomerini appear to take the place of species of *Torymus* Dalman (Torymini), which feature prominently in the parasitoid communities in cynipid galls on *Rosa* (Diplolepidini) and *Quercus* (Cynipini). We provide a key, and review the host associations of the two species of *Adontomerus* and six of *Idiomacromerus* that are parasitoids in galls of Cynipidae. Two new species of *Idiomacromerus* are described.

KEY TO EUROPEAN SPECIES OF *ADONTOMERUS* AND *IDIOMACROMERUS* PARASITIC IN CYNIPID GALLS

1. Antenna with one anellus and 7 funicle segments (with linear sensillae); basal tergite of gaster rather strongly incised medially on its posterior margin; forewing with infuscate spot behind marginal and stigmal veins (*Adontomerus*) 2
– Antenna (Figs. 2, 4) with two (rarely three) anelli (lacking linear sensillae) and 6 (rarely 5) funicle segments; basal tergite of gaster weakly incised on posterior margin; forewing usually without dark spot (present in *mayri*), sometimes with a yellowish mark (*Idiomacromerus*) 3

2. Metafemur of female 2.8× as long as broad ..... ***impolitus*** **(Askew and Nieves-Aldrey)**
– Metafemur of female very stout, 2.2× as long as broad ..... ***crassipes*** **(Bouček)**

3. Body mainly yellow, darker dorsally but without metallic tints; head with tract of flattened, shining white scale hairs around orbit; metatibia with only one distinct apical spur (Fig. 5C); female antenna with a colourless process at apex of clava (Figs. 5A, 5B); male with relatively small eyes 4

– Body dark, metallic, with yellow colouration at most on part of gaster; conspicuous circumorbital tract of white scale hairs absent; metatibia with two apical spurs; female antenna without a colourless apical claval process; male eyes normal 5

4. Ovipositor sheath almost 1.6× as long as metatibia; female gaster (excluding ovipositor) 1.6× as long as mesosoma, gaster plus ovipositor 1.8× as long as rest of body; funicle segments less compacted; larger, female body including ovipositor 3.3mm ..... ***urospermi* sp. n.**
– Ovipositor sheath about as long as, or very slightly longer than, metatibia; female gaster (less ovipositor) 1.1–1.2× as long as mesosoma, gaster plus ovipositor 1.4× as long as rest of body; funicle segments transverse and more compacted; smaller, overall length of female body 2.2mm ..... ***semiaenea* (Szelényi)**

5. Antennal flagellum strongly clavate, the third segment (F1) distinctly narrower than pedicel. (Mesosoma in dorsal view relatively narrow, 1.45–1.5× as long as broad; ovipositor sheath 1.5–1.7× as long as metatibia; metafemur 3.4× as long as broad) ..... ***centaureae* (Askew and Nieves-Aldrey)**
– Antennal flagellum less clavate, F1 from almost as broad to slightly broader than pedicel 6

6. Female gaster with basal tergites dorsally yellowish (mesosoma in dorsal view 1.55× as long as broad; ovipositor sheath 1.4× as long as metatibia; metafemur 2.8× as long as broad) ..... ***silybi* sp. n.**
– Female gaster entirely dark with metallic reflections on basal tergites 7

7. Forewing clear; body dark bronze-green; mesosoma in dorsal view about 1.5× as long as broad; antennal funicle segments distinctly transverse. (Ovipositor sheath 1.6× as long as metatibia; metafemur 2.8× as long as broad) ..... ***papaveris* (Förster)**
– Forewing with dark mark behind marginal vein; body dark bronze with few green reflections; mesosoma in dorsal view 1.2–1.3× as long as broad; antennal funicle segments only slightly transverse ..... ***mayri* (Wachtl)**
[*I. mayri* is not known to us, its characters being taken from the literature]

Adontomerus crassipes (Bouček)

Microdontomerus crassipes Bouček, 1982

A. crassipes has been reared in Spain from galls of *Andricus kollari* (Hartig) (agamic gen.) on *Quercus petraea* and *Q. pubescens*, and galls of *Isocolus lichtensteini* (Mayr) (= *tavaresi* Nieves-Aldrey) on *Centaurea aspera* (Askew and Nieves-Aldrey 1988). The record in Askew and Nieves-Aldrey (1988) of material from the plant *Leuzea* (as *Centaurea*) *conifera* refers to the host *Isocolus leuzeae* Nieves-Aldrey; we have since obtained more specimens from this host. A male from the type series was obtained from an unidentified gall on *Centaurea sphaerocephala* in Algeria.

A. crassipes is one of the few chalcid parasitoids known to attack hosts in cynipid galls on both oak trees and herbaceous plants.

Adontomerus impolitus (Askew and Nieves-Aldrey)

Microdontomerus impolitus Askew and Nieves-Aldrey, 1988

This species is a common parasitoid in Spain in galls of *Aulacidea tragopogonis* (Thomson) which develop concealed inside stems of *Tragopogon*. Recently we have seen many specimens reared from galls of *Aulacidea acroptilonica* Tyurebaev on *Acroptilon repens* collected in Turkey and Uzbekistan, submitted in 2003 by Urs Schaffner (CABI Switzerland).

Idiomacromerus centaureae (Askew and Nieves-Aldrey)

Liodontomerus centaureae Askew and Nieves-Aldrey, 1988

I. centaureae is so far only known as a parasitoid in galls of *Phanacis centaureae* Förster developing inside stems of *Centaurea scabiosa* in Spain. In addition to the type locality in Guadalajara, we have subsequently obtained *I. centaureae* in Cuenca from galled *C. scabiosa* collected 3.v.2002 beside the Tragacete to Uña road.

Idiomacromerus mayri (Wachtl)

Lochites mayri Wachtl, 1883

I. mayri is reported to have been reared from galls of *Aulacidea scorzonerae* (Giraud) in Hungary (Szelényi 1957a; Erdös 1966) and France (Giraud and Laboulbène 1877, as *Callimome scorzonerae* nomen nudum), and *A. tragopogonis* on *Tragopogon* in Hungary (Erdös 1966). Bouček (1995) records *I. mayri* from the Czech Republic.

Idiomacromerus papaveris (Förster)

Lochites papaveris Förster, 1856
Liodontomerus papaveris (Förster)

I. papaveris was described from Germany as a parasitoid of *Aylax papaveris* (Perris), and is now known to be widespread in central and southern Europe, associated with cynipid galls formed in seed capsules of *Papaver*. In addition to *A. papaveris*, host gall wasps are reported as *A. minor* Hartig and *Barbotinia oraniensis* (Barbotin); also, Szelényi (1957a) reports rearing *I. papaveris* from galls of *Xestophanes szepligetii* Balás on *Potentilla* in Hungary.

Idiomacromerus semiaenea (Szelényi)

Lochitomorpha semiaenea Szelényi, 1957b

Lochitomorpha Szelényi was synonymized under *Pseuderimerus* Gahan by Grissell (1995) but Zerova and Seryogina (1999) place the present species in *Idiomacromerus*. Our reasons for following the latter authors are explained below under *I. urospermi*. The holotype has been examined (Natural History Museum of Hungary, Budapest). We have two specimens reared from *Centaurea* stems containing galls of *Phanacis centaureae* Förster, collected in Spain (Madrid, Dehesa de Arganda, 5.x.1994, F. Ronquist), but it is not certain that they emerged from the cynipid galls.

Idiomacromerus silybi Askew, sp. n.

Female.—Head and thorax green, dorsally slightly to quite strongly coppery, bronze tints on sides of thorax, not very shining; gaster with three basal tergites dull yellow, otherwise brown with very faint metallic tints, ovipositor dark brown. Head with a narrow band of shining white, flattened scale hairs on lower inner orbit. Scape testaceous ventrally and basally, dark brown in upper part; pedicel weakly metallic; flagellum brown. Legs with coxae more or less testaceous apically but otherwise dark metallic green with copper reflections; femora mostly brown; rest of legs brownish yellow with tarsal claws brown. Tegula testaceous, darker centrally; forewing clear, venation pale. Length of holotype, excluding ovipositor, 2.2mm, ovipositor sheath 0.8mm; in small specimens the overall body length is barely 2 mm.

Head in dorsal view 1.25× breadth of mesoscutum, 2.2× as broad as long; POL 2.4× OOL, posterior ocellus separated from orbit by about 1.75× its diameter. Head in front view 1.27× as broad as high, malar space 0.5× height of eye; torulus with ventral edge slightly above level of lower orbit; scrobes moderately deep, mesially confluent above intertorular prominence. Occiput without carina. Antenna (Fig. 2) with scape not reaching level of anterior ocellus by one major diameter of latter; length of pedicel plus flagellum 0.87× head breadth; pedicel about 2.5× as long as broad, almost to fully as long as first four flagellar segments, with many

short hairs; flagellum clavate with two anelli and six moderately compact funicle segments (in small specimens F1 may be scarcely longer than the second anellus, narrower than the pedicel, and apparently lacking linear sensillae); F1 from almost as broad to slightly broader than pedicel at apex, broader than long as F2–F6; clava about 2× as long as broad, apically rounded without process or spicule; linear sensillae inconspicuous in a single transverse row on each segment, hairs on flagellum short and not outstanding.

Mesosoma in dorsal view 1.55× as long as broad; pronotum with dorsal surface rounded into anterior face; mesonotum dorsally with inconspicuous, short, white pilosity, the hairs somewhat flattened (scale hairs), reticulate sculpture raised and fine; notauli complete but not deep; scutellum as broad as long; propodeum medially 2× as long as dorsellum, its anterior margin with a row of small foveae (10 in holotype) separated by carinulae, smooth and shining medially but with faint, fine reticulate sculpture laterally. Posterior leg with dorsal surface of coxa sparsely and shortly pilose; femur 2.8× as long as broad; tibia with two distinct apical spurs, the outer about half as long as the inner.

Forewing (Fig. 1) basal cell with only 1–3 hairs (excluding hairs on basal and cubital veins); speculum partially open below; lengths of costal cell: marginal vein: stigmal vein: postmarginal vein as 70:34: 11:19; marginal plus postmarginal veins occupying 0.31× wing length.

Gaster (Fig. 1) (excluding ovipositor) slightly shorter than head plus mesosoma; basal tergite with posterior margin weakly incised medially; tip of hypopygium at 0.75× gaster length; ovipositor sheath 0.73× as long as rest of gaster, 1.4× length of metatibia.

Male.—Unknown.

Holotype. ♀. SPAIN, Madrid, Dehesa de Arganda, e× gall *Aulacidea freesei* Nieves-Aldrey in stem of *Silybum marianum* (L.), collected 6.XI.2002, emerged 2003 (R. R. Askew). Depository Museo Nacional de Ciencias Naturales, Madrid.

Paratypes. 2♀♀. Same data as holotype.

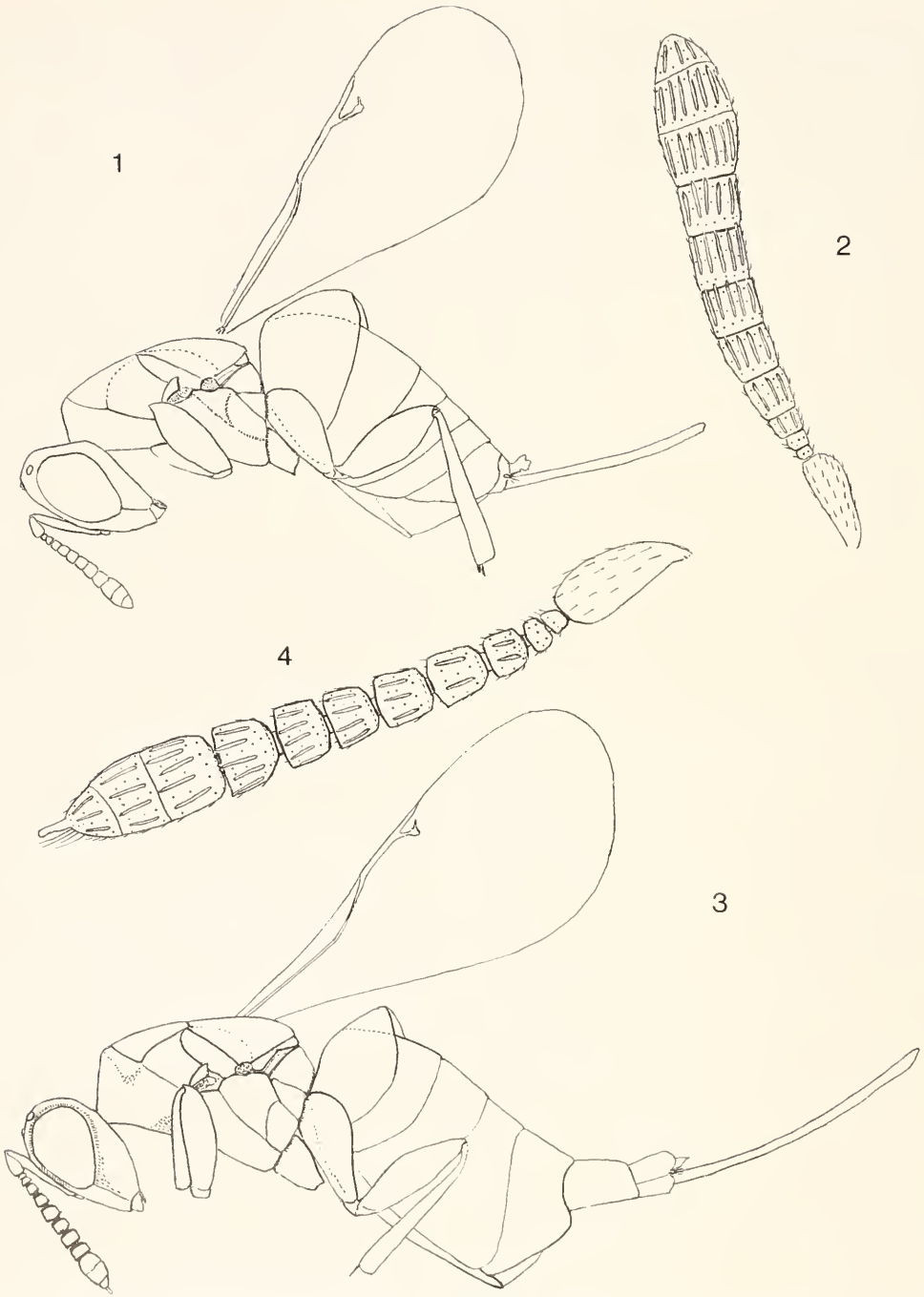
Additional material. 3♀♀. SPAIN, Málaga, Torcal de Antequera, e× stems *S. marianum* with galls of *A. freesei* or *Phanacis zwoelferi* Nieves-Aldrey, collected 17.VIII.2002 (J.L. Nieves-Aldrey).

Biology.—A parasitoid in galls of *Aulacidea freesei* (Hym., Cynipidae) developing in stems of *Silybum marianum*. Galls of *Phanacis zwoelferi* Nieves-Aldrey also develop in *Silybum* stems and it is possible that these too are attacked by *I. silybi*. The final instar larva of *I. silybi* is described below.

Comments.—*I. silybi* bears a strong resemblance to *I. papaveris* in colour and sculpturation of head and thorax, and in antennal structure and wing venation. The two species may be easily distinguished however by the extensive area of dull yellow colour on the dorsal surface of the basal tergites of the gaster in *I. silybi*, this region being entirely dark in *I. papaveris*. Additional differences are indicated in the key (above).

Final instar larva (Fig. 5D).—The last instar larva is typically hymenopteriform. It is apodous and measures about 2–2.5 mm. in length and less than 1 mm. in breadth. The colouration is whitish and the shape is cylindrical, slightly flattened dorso-ventrally, longitudinally elongated and clearly narrowed at posterior end. Tegument smooth but with rows of long, erect setae which are as long as length of one ring segment. Setae are lacking on the ventromedial part of body. The larva possesses a distinct head and 13 body segments.

Head in anterior view (Fig. 5E) 1.2× as broad as high. Mouthparts are protruding. Vertex with at least 12 long, strong setae which are nearly as long as half the distance between the antennae. The two antennal setae are long, each situated above an antenna at a distance equal to its length. Two narrow tracts of shorter setae



Figs. 1–4. *Idiomacromerus silybi* Askew sp. n. 1) adult female, 2) female pedicel and flagellum. *I. urosperni* Askew sp. n. 3) adult female (paratype), 4) female pedicel and flagellum.

run from the vertex to near the clypeus, separated by a narrow, smooth strip. The surface of the face below and lateral to the antenna is vesiculous. Antenna are small and separated by a distance about two times as long as the distance between an antenna and the lateral margin of the head. The two genal setae are very long, extending far below the level of the mouthparts.

Clypeus indistinct, its ventral margin straight, medially bearing a pair of clypeal setae. Labrum flexed along its ventral margin and laterally with a pair of papillae. The maxillae are small and more or less triangular, bearing a pair of indistinct palps. Labium concave without visible setae or palps. Mandibles simple, each with a single, acute tooth.

Idiomacromerus urospermi Askew, sp. n.

Female.—Head and thorax dull yellowish to brown without metallic colouration, darkest on thoracic dorsum. Head with vertex and frons red-brown, shading to straw-coloured on lower face, gena and occiput; mandible dark brown, palps very pale; tracts of closely spaced, silvery white scale hairs on inner and outer orbits, intertorular prominence and area between scrobes, laterad of scrobes and in a patch between torulus and eye. Scape and pedicel red-brown; flagellum dorsally light brown, the basal two claval segments darker, flagellum ventrally straw-coloured; claval tip with a whitish digitiform extension, and tuft of dark setae (partly as described by Szelényi (1957b) for *I. semiaenea*). Pro- and mesonota dark red-brown to chocolate coloured; sides of thorax below level of wing insertions shading to pale brownish yellow; metathorax, propodeum and gaster almost entirely yellow except for brown ovipositor sheath. Legs light brown, coxae palest and tarsal claws darker brown. Forewing with a yellowish discal area, colour deepest behind marginal and stigmal veins; venation pale. Length excluding ovipositor 2.4mm., ovipositor sheath 1.0mm.

Head in dorsal view 1.3× breadth of mesoscutum, 2× as broad as long; POL 1.8× OOL, posterior ocellus separated from orbit by about 2.5 diameters. Head in front view 1.35× as broad as high; malar space 0.66× height of eye; torulus with dorsal edge about on a level with lower orbit; scrobes deep, converging upwards so that inner margins meet about two ocellar diameters below anterior ocellus, separated by wedge-shaped prominence outlined by white scale hairs. Occiput without carina. Antenna (Fig. 4) with scape just reaching lower margin of anterior ocellus; length of pedicel plus flagellum 0.9× head breadth; pedicel 2× as long as broad, longer than the combined length of the basal three flagellar segments; flagellum strongly clavate, first two segments anelliform, transverse, without linear sensillae; third flagellar segment (first funicle, F1) about as broad as pedicel at apex and slightly broader than long, about 2× as long as second anellus; following funicle segments progressively broader and slightly longer, separated by short petioles and not compacted, F6 1.7× as broad as F1; clava slightly less than 2× as long (excluding apical process) as broad, the digitiform apical process only slightly shorter than third claval segment (Fig. 5A) and situated above a tuft of long setae which each terminate in a short filamentous process (Fig. 5B); linear sensillae distributed on flagellum as in Figure 4.

Mesosoma in dorsal view 1.55× as long as broad; pronotum with anterior face angularly separated from dorsal face, the latter with dense vestiture of relatively long, white scale hairs; mesonotum dorsally with shorter white scale hairs, very fine reticulate sculpture, lustreless, notauli deep, scutellum 1.1× as long as broad; propodeum medially 2× as long as dorsellum, its anterior margin with short carinulae separating small foveae behind dorsellum. Legs with metacoxa pilose on

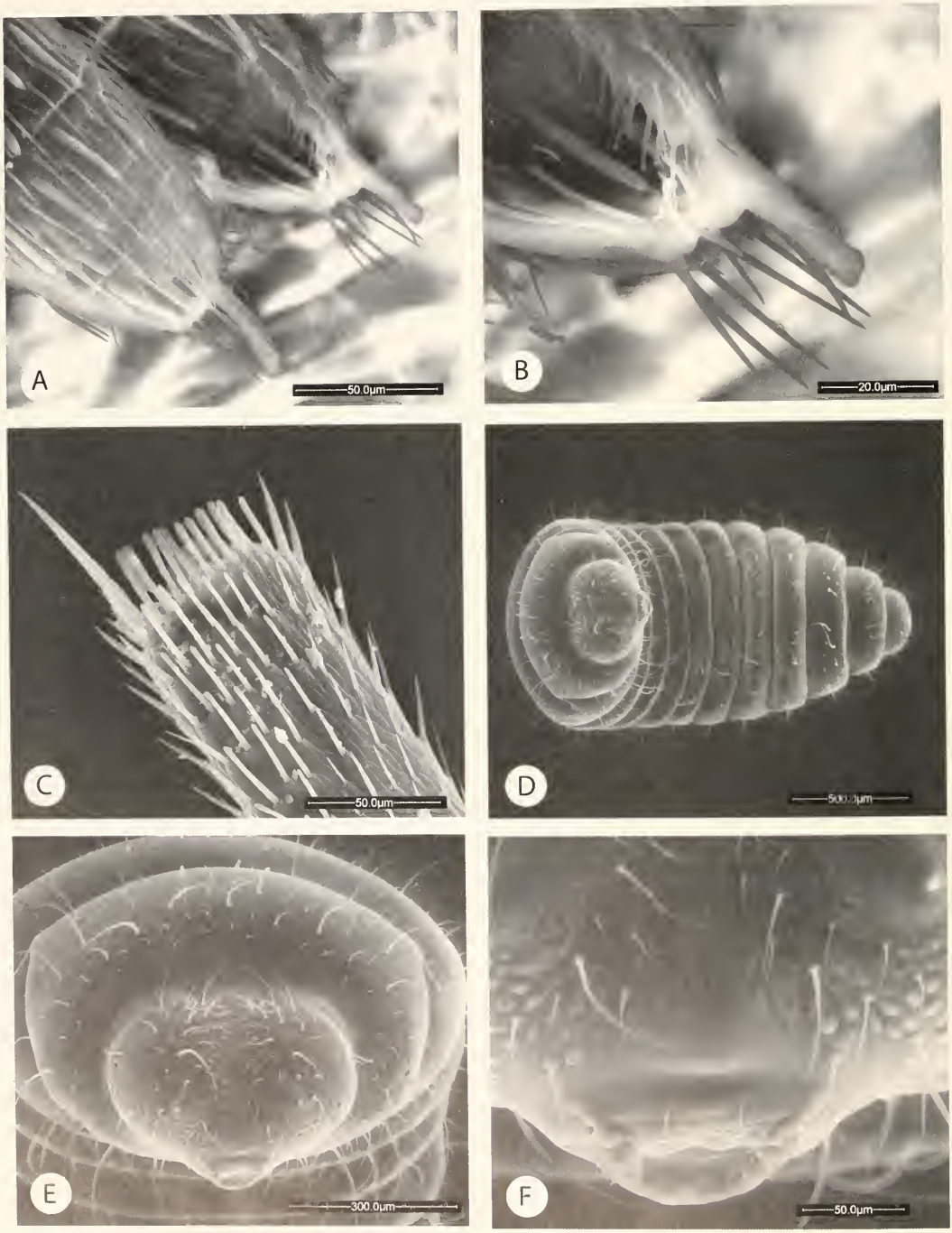


Fig. 5. *Idiomacromerus urosperni* Askew sp. n. adult female A) second and third claval segments of both antennae, B) apex of left clava, inner aspect, C) apex of metatibia. *I. silybi* Askew sp. n. final instar larva D) ventral view, E) head and first body segment, anterior view, F) oral region.

dorsal surface; femora rather stout, the metafemur almost 3× as long as broad; metatibia with only one apical spur (Fig. 5C).

Forewing (Fig. 3) with basal cell pilose but hairs pale and difficult to see; relative lengths of costal cell: marginal vein: stigmal vein: postmarginal vein as 82:32:9:16; marginal plus postmarginal veins occupying 0.25× wing length.

Gaster (Fig. 3) excluding ovipositor 1.25× as long as head plus mesosoma; basal tergite with moderate incision medially on posterior margin; tip of hypopygium at 0.6× gaster length; ovipositor sheath 0.75× as long as rest of gaster and 1.58× length of metatibia.

Male.—Unknown.

Holotype. ♀. SPAIN, Malaga, Casares, ex gall of *Timaspis urospermi* Kieffer in stem of *Urospermum picroides* (L.), collected 20.viii.2002, emerged 16.ix.2003 (J. L. Nieves-Aldrey). Deposited in Museo Nacional de Ciencias Naturales, Madrid.

Paratype. 1♀. Same data as holotype except date of emergence ix.2002.

Additional material. 1♀. Same data as holotype except emergence date x.2002. This specimen was lost in a car theft.

Biology.—All known specimens were reared from galls of *T. urospermi* (Hym., Cynipidae) in stems of *Urospermum picroides.*

Comments.—*I. urospermi* is closely allied to *I. semiaenea* (above) and these species are distinguishable from other *Idiomacromerus* associated with cynipid galls by the body being extensively reddish yellow to red-brown, darker on dorsal surface, and dull with very fine reticulate sculpture. There are several areas of silvery white scale hairs, these being especially apparent in an almost complete circumorbital ring. The antennal clava bears a white apical process and the metatibia has only one apparent apical spur. These two latter features are characters of the genus *Pseuderimerus* Gahan, but *I. urospermi* and *I. semiaenea* more closely resemble other species of *Idiomacromerus* than they do Palaearctic *Pseuderimerus.* In the European *P. luteus* Bouček the spicule at the tip of the antennal clava appears to be of different structure to that of *I. urospermi* and *I. semiaenea,* the eyes and ocelli of female *P. luteus* are small (height of eye slightly less than length of antennal scape, posterior ocellus separated from adjacent orbit by about three ocellar diameters; in female *Idiomacromerus* the eye is longer than the scape and the posterior ocellus is separated from the orbit by scarcely twice its diameter), and *P. luteus* is entirely pale yellow without a vestiture of white scale hairs. We therefore follow Zerova and Seryogina (1999) in regarding *I. semiaenea* (and *I. urospermi*) as species of *Idiomacromerus* rather than *Pseuderimerus.*

I. urospermi is distinguished from *I. semiaenea* by its relatively longer ovipositor and gaster, and longer antennal flagellum, as detailed in the key.

ACKNOWLEDGMENTS

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The Enigmatic Biology of the Ichneumonid Subfamily Lycorininae

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Abstract.—Females of *Lycorina apicalis* Cresson and *L. marvini* Gauld (Ichneumonidae: Lycorininae) were dissected and found to have pedunculate eggs with an 'anchor' at the tip, similar to those of Tryphoninae. Several differences are noted between Tryphoninae and Lycorininae and thus no close relationship is indicated. Observations of *L. apicalis* reared from a larva of *Omiodes indicata* (Lepidoptera: Crambidae) demonstrate that this species is a koinobiont that finishes its development as an ectoparasitoid. However, we were unable to locate the early larval stages of the parasitoid on the exterior of the host.

Key words.—*Lycorina*, *Omiodes*, Crambidae, egg morphology, koinobiont, ectoparasitoid, Costa Rica

The Lycorininae is a small subfamily of Ichneumonidae composed of 28 species classified in a single genus, *Lycorina* Holmgren (Yu and Horstmann 1997). The monophyly of the group is supported by several unusual synapomorphies, including the unique metapleural catch (Gauld 1984), raised and clearly defined triangular areas on tergites II–IV, and possession of a large triangular subgenital plate in the female which is weakly sclerotized in the central part. The group is cosmopolitan, but unlike most other subfamilies of Ichneumonidae it is most species rich in the tropics and the southern hemisphere (Yu and Horstmann 1997). The phylogenetic relationships of the Lycorininae are poorly understood. Townes, in his various reclassifications of the Ichneumonidae initially placed it as a tribe in the Banchinae (Townes and Townes 1951), later as a genus in the banchine tribe Glyptini (Townes and Townes 1966) and finally, on the basis of information about the larva, as a distinct subfamily next to the Banchinae (Townes 1970). However, the characters supporting a relationship with the Banchinae appear to be symplesiomorphies (Gauld 1984) so the phylogenetic placement of this group remains uncertain.

Compounding this uncertainty is the fact that very little is known of the biology of the group, and it is not known for certain whether species are ecto- or endoparasitic, koinobiont or idiobiont (Gauld 1997). Although there are comparatively few rearing records, the focal host range of lycorinines seems to be the weakly concealed larvae of microlepidopterans. Some species from north temperate regions have been reared from pyralid leaf-rollers and leaf-tiers (Doerksen and Neunzig 1974, Finlayson 1976), and from tortricids (Chao 1980). Of the eight species found in Costa Rica only one, *L. apicalis*, has been reared. Previous host records for this species include an undetermined species of *Lamprosema* Hübner (Crambidae: Pyraustinae) (Gauld 1997) and the prepupa of *Ethmia catapeltica* Meyrick (Ethmiidae) (Janzen and collaborators: *http://janzen.sas.upenn.edu/*). Recently we reared this same species from *Omiodes indicata* (Fabricius) (Cram-

bidae: Pyraustinae), collected in May, 1996, in leaf-rolls of beans (*Phaseolus vulgaris* L.), in a field located in Turrialba, Costa Rica.

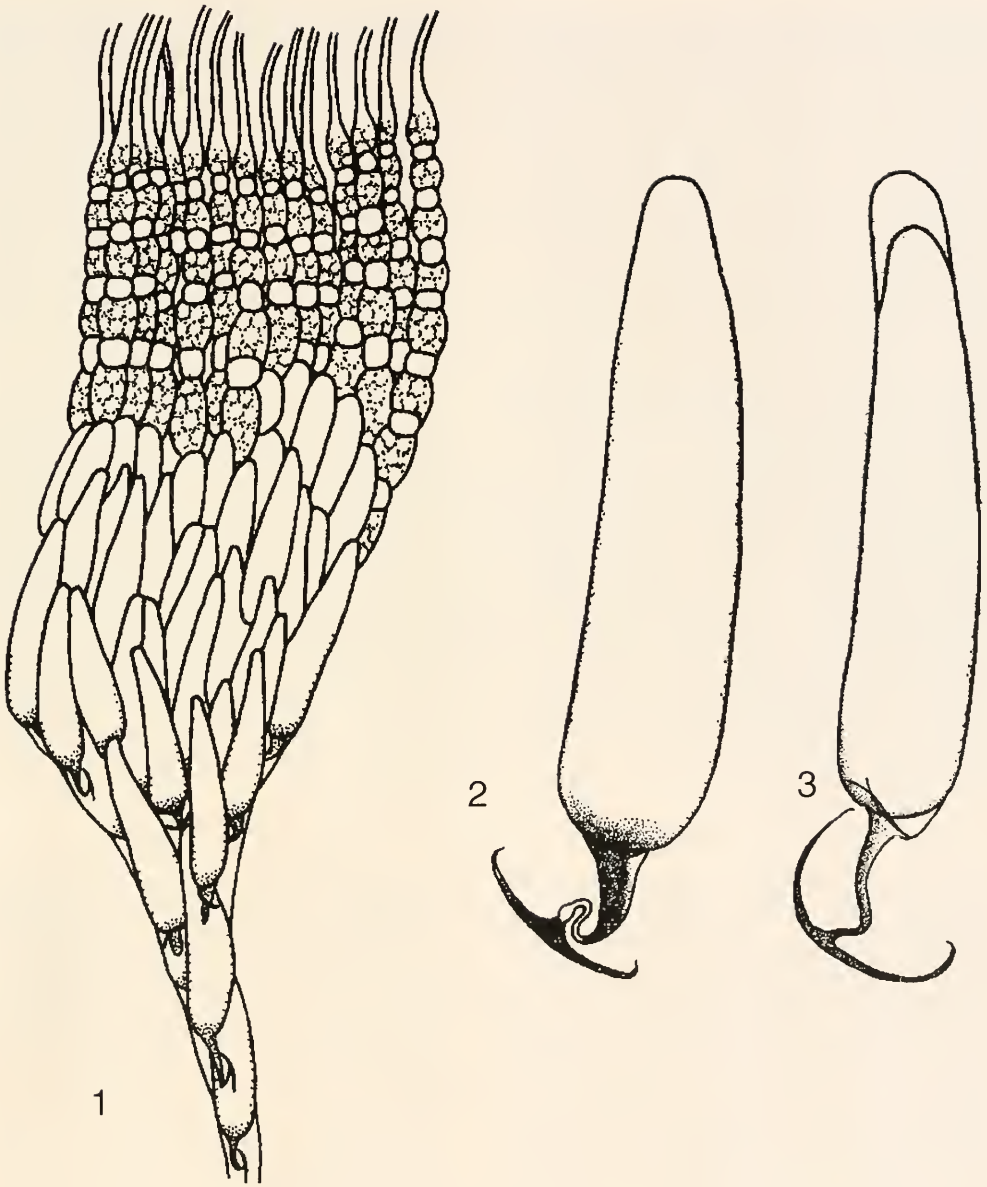
The head capsule of the final instar larva is enigmatic, possessing features of both ectoparasitic and endoparasitic species. For example, the mandibular teeth are denticulate, similar to some other ectoparasitic ichneumonids such as Tryphoninae and Cryptinae (Finlayson 1976, Short 1978, Chao 1980, Gauld 1997). Nonetheless, some endoparasitic braconids such as Microgastrinae, which emerge from their hosts in the final instar in order to complete their development by feeding externally, have a similar mandibular tooth (Capek 1973). On the other hand, in contrast to many ectoparasitoids, the larvae of Lycorininae lack a distinctive labral sclerite, have a disc-like antenna, and the spiracle lacks a closing device, all of which suggest that the larva is possibly endoparasitic (Gauld 1997).

In this note we present some new observations on the biology and anatomy of these enigmatic insects, which complement recent observations on a European species of *Lycorina* (Shaw 2004). Voucher specimens are deposited in the Insect Museum of the University of Costa Rica (IM-UCR, San Pedro) and in the National Biodiversity Institute (INBIO, Santo Domingo).

Egg Morphology

Four female specimens of *L. apicalis* Cresson and two of *L. marvini* Gauld, (collected in Malaise traps from various sites in Costa Rica), were dissected to observe the morphology of the ovaries and eggs. In both species the eggs are elongate-oval, with a chitinized chorion, and lightly sclerotized at the apex in *L. apicalis*. Remarkably, the eggs of both species have a long, thin, and flexible peduncle with an "anchor" at the apex, although the exact form of the anchor varies between the two species (Figs. 2–3). Possession of stalked eggs with an anchor-like end is elsewhere, in Ichneumonidae, only known within the subfamily Tryphoninae (Bennett 2002). However, there are several notable differences between the eggs of Lycorininae and Tryphoninae. Those of the latter subfamily are much larger (1.06–0.24 mm in length, avg. = 0.64; 0.41–0.09 mm in width, avg. = 0.27; data from Iwata, 1958, based on 10 species in 5 tribes) compared with the small eggs of *L. apicalis* (0.5 mm in length; 0.1 mm in width) and *L. marvini*: (0.6 mm in length; 0.1 mm in width), and tryphonine eggs have a strongly sclerotized chorion (Iwata 1960, Kasparyan and Tolkanitz 1999). Moreover, in many tryphonines the anchor, not the egg, travels down the lumen of the ovipositor (Kasparyan 1981). The egg is attached externally to the host by the anchor which is pushed through the host's cuticle by the ovipositing female ichneumonid (Simmonds 1947, Baltensweiler and Moreau 1957, Pschorn-Walcher 1967, Beingolea and Vásquez 1994). In many female tryphonines an egg is visible beneath the base of the ovipositor. We have examined over 100 individuals of *Lycorina* collected in Costa Rica but never observed an egg in a similar situation, which suggests that perhaps the egg travels down the lumen of the ovipositor in the normal ichneumonid manner.

The only published study of the eggs of species in this subfamily (Iwata 1958) described the eggs of the Palaearctic species, *L. triangulifera* (Holmgren), as being leech-shaped. Although Iwata's description differs from our observations, Shaw (2004) has recently found that the eggs of *L. triangulifera* do in fact have an anchor, which agrees with our results. Our observations are similar to those of Iwata (1960) in that the ovaries of all lycorinine species are characterized by having high numbers of ovarioles: *L. apicalis* (10–19 per ovary) (Fig. 1); *L. marvini* (13–27 per ovary); *L. triangulifera* (18–25 per ovary), with many small eggs, 13–23 per ovary in *L. apicalis*,



Figs. 1–3. Ovaries and eggs of *Lycorina*. 1, Ovary of *L. apicalis*. 2, Egg of *L. apicalis*. 3, Egg of *L. marvini*.

30–40 per ovary in *L. marvini* and 32–64 per ovary in *L. triangulifera*.

The similarity in egg structure among the three species that have been observed suggests that lycorinines share a similar developmental biology. The pedunculate, anchored egg of Tryphoninae has been considered to be an adaptation for ectoparasitism (Bennett 2002), but several observations suggest that lycorinines are endoparasitoids, or at least begin their development as endoparasitoids. The form of the ovaries of *Lycorina* are more similar to those of endoparasitic koinobiont ichneumonids than they are to those of ectoparasitic koinobionts or idiobionts. The data of Iwata (1960), who examined 1,397 specimens representing 376 species of Ich-

neumonidae, suggest that the ovaries of idiobionts and ectoparasitic koinobionts tend to have rather few ovarioles (idiobionts: 2–15 per ovary; ectoparasitic koinobionts: 3–8 per ovary) and a reduced number of relatively large, mature eggs (idiobionts: 2–14 per ovary; ectoparasitic koinobionts: 3–10 per ovary). In contrast, endoparasitic koinobionts tend to have a large number of ovarioles (3–59 per ovary) and a large number of relatively small, mature eggs (24–111 per ovary). In the three species of *Lycorina* in which the ovaries have been described, there are 10–27 ovarioles per ovary, and the mature eggs are relatively small and numerous (13–64 per ovary). Thus, both the structure of the ovaries and the size of the eggs suggest that lycorinines are endoparasitic koinobionts. However, it should be kept in mind that the above comparisons do not take into account phylogenetic dependence (e.g. in Tryphoninae, the low number of ovarioles and eggs could simply be the ancestral condition).

Larval Development

In the specimen of *L. apicalis* that we reared from a larva of *Omiodes indicata*, the parasitoid larva was not observed until eight days after the caterpillar had been collected. At that point the larva of *L. apicalis* was observed feeding as an external parasitoid, just as the caterpillar was beginning to spin its cocoon. Although we cursorily examined the host larva prior to this, we failed to notice any external parasitoid or externally positioned egg. The adult parasitoid emerged 21 days after having eaten the host. The remains of the host were examined under a dissecting microscope to see if there were remains of an externally deposited egg, but none were found.

Although the above observations are consistent with development being initially endoparasitic, the recent discovery that the egg of *L. triangulifera* is deposited through the anus of the host (Shaw 2004) explains why we failed to observe young larvae, and also suggests that early development could possibly occur as an ectoparasitoid in the hindgut. Both our results and those of Shaw (2004) demonstrate that lycorinines are koinobionts, and our observations show that development is completed as an ectoparasitoid. However, whether the young larvae are ectoparasitic (presumably in the hindgut), or endoparasitic, remains to be demonstrated.

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A New Species and Host Association Biology of Neotropical *Compsobraconoides* Quicke (Hymenoptera: Braconidae)

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Abstract.—The new species ***Compsobraconoides cinnamomi*** **Fortier and Nishida** is described from Costa Rica. Specimens were obtained from galls on lower branches of *Cinnamomum cinnamomifolium* (Kunth) Kosterm that were caused by *Camptocheirus* Lacordaire (Coleoptera: Curculionidae). *Compsobraconoides* larvae were observed feeding on *Camptocheirus* larvae in galls.

Resumen.—La nueva especie ***Compsobraconoides cinnamomi*** **Fortier and Nishida** es descrito para Costa Rica. Especimenes fueron obtenidos de agallas en ramas de árboles de *Cinnamomum cinnamomifolium* (Kunth) Kosterm. Las agallas son inducidas por una especie de *Camptocheirus* Lacordaire (Coleoptera: Curculionidae). Larvas de *C. cinnamomi* fueron observadas alimentándose de larvas de *Camptocheirus* sp. en agallas.

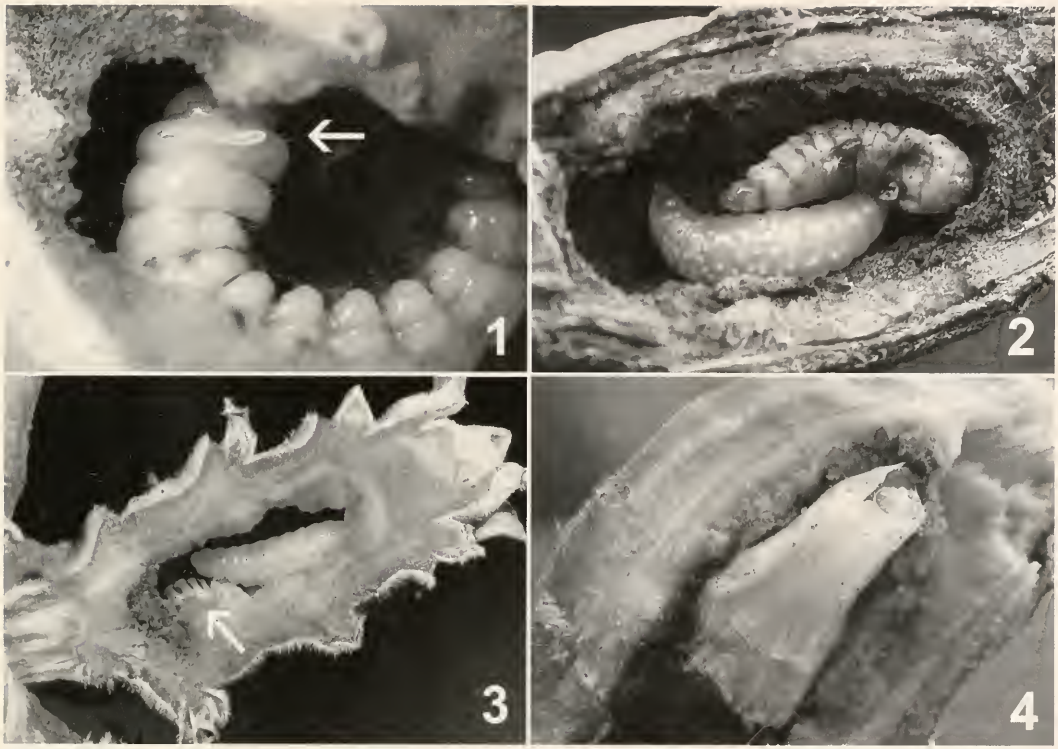
Of the cosmopolitan braconid subfamily Braconinae, which is composed of about 200 genera and 5000 species worldwide (Quicke 1988, Quicke and Sharkey 1989), *Compsobraconoides* Quicke is a moderately large, principally neotropical genus, occurring from the southern U.S. to South America including the Caribbean. The genus was erected by Quicke (Quicke and Sharkey 1989). A new species has been described by Quicke (Quicke and Sharkey 1989), as well as the new combination *Compsobraconoides albispina* (Cameron), formerly *Bracon albispina* Cameron.

Braconine females usually oviposit through substrate containing the host, usually attacking late larval instars. Hosts usually are concealed within living plant tissue, such as tree bark, stems of annual and biennial plants, galls, and seed heads. Some braconines attack casebearing hosts (Shaw and Huddleston 1991). Most braconines are idiobiont ectoparasitoids, and eggs are generally laid on the host's body, although first instar larvae are able to travel short distances to locate their hosts if necessary (Shaw and Huddleston 1991).

Prior to this study, one host record existed for an unidentified *Compsobraconoides* species from three species of *Azteca* ants (Dolichoderinae) colonizing domatia of *Cordia nodosa* Lam. (Boraginaceae) in Peru (Yu & Quicke 1997). This study represents the first host record for a described *Compsobraconoides* species, and the first association of a *Compsobraconoides* species with Coleoptera. Both host associations involve hosts in swollen plant tissue. Since *Azteca* ants do not occur in the United States, while *Compsobraconoides* does, it was obvious that *Compsobraconoides* must have other hosts.

MATERIALS AND METHODS

Galls induced by *Camptocheirus* Lacordaire sp. were collected in August and September, 2000, January, February, and June to August, 2001, and May, June, September, and November, 2002. Collections were made on the campus of the Univer-



Figs. 1–4. Biology of early stages of *Compsobraconoides cinnamomi*. 1, Egg located on third instar host larva (arrow). 2, Late instar *C. cinnamomi* larva feeding. 3, Mature last instar larva in host gall chamber (note arrow showing remaining host cadaver). 4, Pupa *in situ* (note one end of cocoon removed showing head).

sity of Costa Rica (elevation: 1150 m.) in San Pedro, San José, Costa Rica. The habitat on which the university campus is located was considered to be a moist premontane tropical forest (Holdridge 1967). However, it is now a large urbanized part of San José. The surrounding area is therefore highly altered. A few coffee plantations still remain in the area. Identification of *Camptocheirus* was made by C. H. Lyal, The Natural History Museum, London.

Stems with mature galls were collected from lower branches (approximately three to five m. from the ground) of three *Cinnamomum cinnamomifolium* (Kunth) Kosterm (Lauraceae) trees (height: ca. 15 m, tree base diameter ca. 77 to 184 cm) and were carried back to the entomological laboratory of the university (average room temp. 23 to 24 °C). The collected galls (about 120) were split in half longitudinally and observed. The galls were resealed when presented in any stage of the parasitoid (Figs. 1–4), and these were reared in transparent plastic bags.

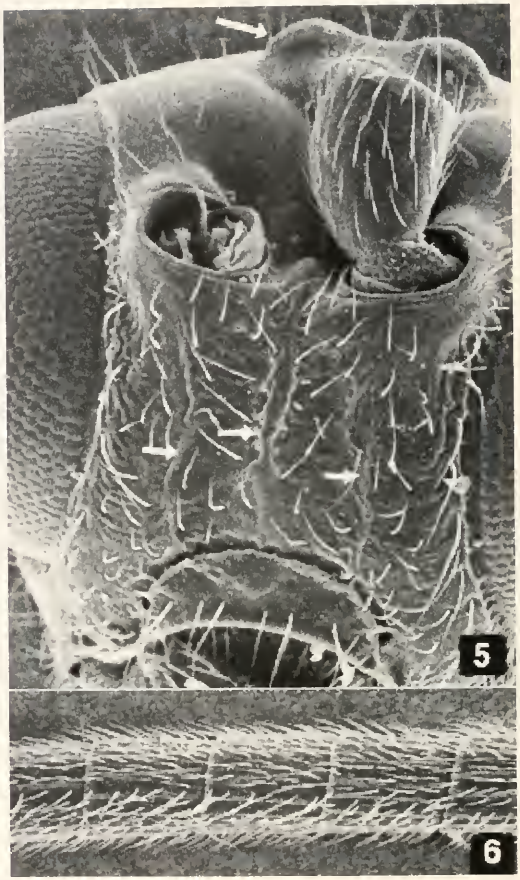
RESULTS AND DISCUSSION

Two relatively small *Compsobraconoides cinnamomi* larvae (apparently late first or early second instar) were found attached to an immobile mature *Camptocheirus* larva in a gall that was collected on October 29, 2002. On November 2, 2002, only one larva was observed attached to the host larva and it measured ca. 5.5 mm (Fig. 2). The other larva did not survive. Six days later, on November 4, 2002, the *Compsobraconoides* larva appeared to finish feeding on the host, i.e. the larva was not attached to the host larva (Fig. 3). On November 5, 2002, the parasitoid larva began to spin the cocoon in the gall chamber. At

this time, the larva was approximately 6.5 mm long. The larva pupated within a few days; however the pupa did not survive until adult formation. From another rearing record, the pupal stage took approximately 10 days. A more or less recently developed pupa (Fig. 4) was collected on October 29, 2002; and the *Compsobraconoides cinnamomi* adult was flying in the plastic bag on November 6, 2002.

Evidently the adult chews through the hard gall wall in order to emerge from the gall. The gall wall was approximately 4–5 mm thick, fibrous, and relatively hard. A few dead adult *Compsobraconoides cinnamomi* individuals were observed in the gall. The time between the adult emergence and the emergence from the gall may possibly take more than a week since the host adult, *Camptocheirus* sp., takes five to fourteen days to tunnel.

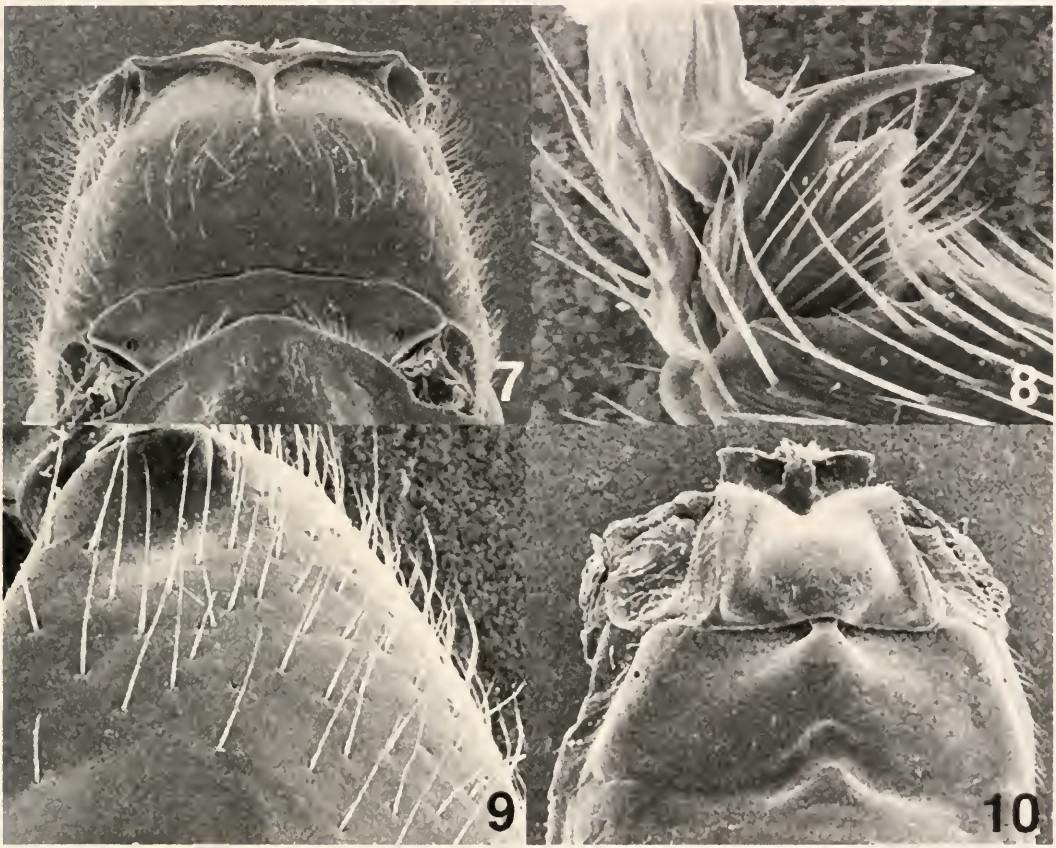
We estimate that approximately 10% of total (120) galls collected contained *Compsobraconoides cinnamomi*. However, fourteen mature galls were collected on May 10, 2003 of which six were parasitized by *C. cinnamomi*.



Figs. 5–6. Head characteristics of *Compsobraconoides cinnamomi*. 5, Face. Note top arrow indicating small ocellus. Other arrows indicate facial carinae. 6, Flagellomeres.

Compsobraconoides cinnamomi Fortier and Nishida, new species
(Figs 5–11)

Female.—Body color: nearly uniformly honey yellow, head black except for yellow clypeus, labrum, mandibles; mandibular tips black; yellow rim at dorsal eye margin; black antennae except yellow base of first flagellomere; front and middle legs with yellow coxae, trochanters, trochantelli, and tarsi, dark brown or black femora, tibiae brown or black except yellow at basal ends, hind coxae, trochanters and trochantelli honey yellow, hind femora honey yellow, hind tibiae, tarsi dark brown or black; wings dusky, stigma medium brown with white tip at basal margin, veins medium brown basally becoming lighter apically, fore-wing vein r-m unpigmented. Body length: 5.3–7.5 mm. Head: malar space shorter than basal width of mandible and about 0.25 length of eye; oral opening height 0.9 of width, width twice length of malar space, face shiny rugulose, three ridges, two extending from antennae to clypeus, one medial (Fig. 5); 39–43 flagellomeres, all slightly longer than wide (Fig. 6), ocelli small, diameter of postero-lateral ocellus less than ocell-ocular space (Fig. 5); frons nitid, sulcus running from point between anterior bases of antennae to anterior of anterior ocellus, bifurcating into two sulci that each terminate at points ventro-lateral of posterior ocelli; vertex, temples, and occiput nitid; palpus not swollen; mandibular tips overlapping when closed. Mesosoma:



Figs. 7–10. Mesothoracic and metathoracic structures and appendages. 7, Propodeum. 8, Hind tarsal claw. 9, Dorsal surface of hind coxa. 10, First and second metasomal tergites.

pronotum nitid, a sulcus on either side of antero-medial ridge running ventro-laterally, terminating at points in antero-lateral areas of pronotum, directly anterior to tegulae, posterior margin on each side of pronotum with a single notch about midway between where pronotum touches tegula and postero-ventral extremity of pronotum; scutum, scutellum nitid, notauli unsculptured, transverse scrobiculate sulcus dividing scutum and scutellum; mesopleuron nitid, broad sulcus running from point near pronotal notch to dorsalmost point of mesopleuron, anterior edge of sulcus carinate; metapleuron, propodeum smooth-punctate with long, silky white setae, median longitudinal carina in apical half or third (Fig. 7). Legs: tarsal claws without pectination but with somewhat pointed basal lobe (Fig. 8), inner spur of hind tibia about 0.5 length of hind basitarsus, hind coxa smooth-punctate with long, silky white setae (Fig. 9). Wings (Fig. 11): second submarginal cell of forewing elongate; 3RSa about 0.65 of 2M; vein r 0.4 length of 3RSa; 1cu-a contiguous with 1M; hindwing RS recurved, not reaching wing margin apically, thus marginal cell open, narrowest apically; 1RSa, 1RSb, r absent, thus RS runs basally to join R at costal cell, R1 ending just before wing apex; sub-basal cell small, M+CU 0.4 of M. Metasoma: all tergites nitid, translucent, 1st metasomal tergite quadrate, lateral flanges extending along lengths of sides of tergite, over spiracles, raised rounded structure in apical half of tergite, increasingly raised over surface of tergite

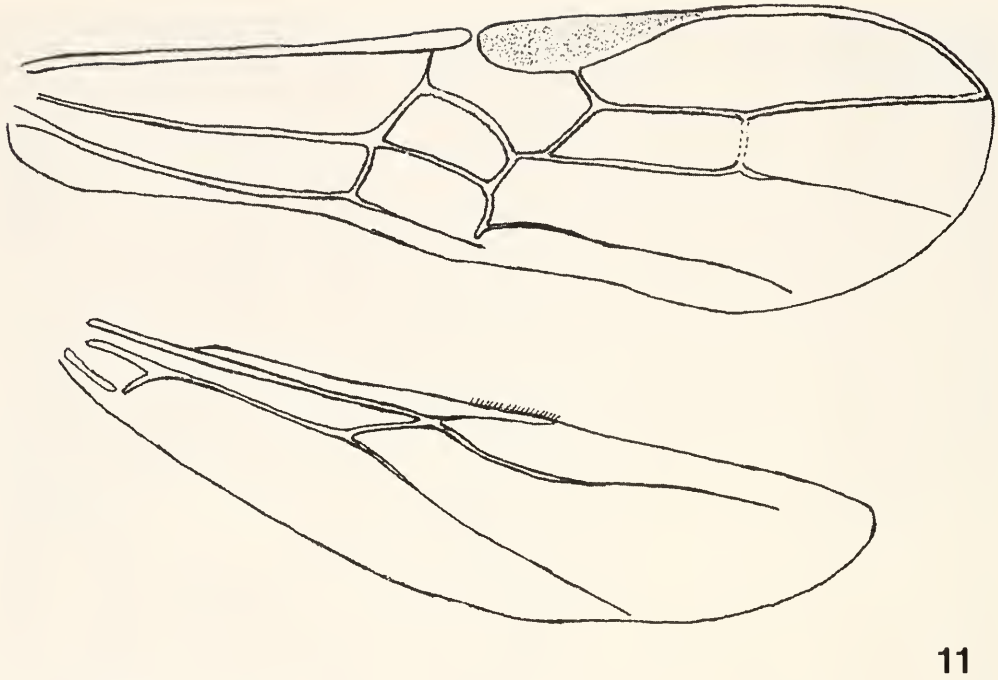


Fig. 11. Wings.

apically, highest point just basal of median point of apex (Fig. 10), 2nd metasomal tergite articulating with first by anteriorly projecting medial process that inserts under apical edge of rounded structure of first tergite, wide medial rounded notch in medial area of apex of 2nd tergite, 3rd tergite evenly convex, 4th and 5th tergites evenly, but more acutely convex, both with wide, shallow tranverse sulcus, 8th abdominal tergite with dark-brown cerci, cerci with long dark setae, setae longer than cercus, each cercus 0.06 mm. Ovipositor: about as long as metasoma, ovipositor sheath black with black setae along entire length.

Male.—Essentially as in female, except humeral plate black medially, in some tegula also black, Body length: 5.3–5.6 mm.

Holotype female.—COSTA RICA: San Jose, San Pedro, UCR campus, 1150 m., 30/V/2002–21/X/2002, ex: larva *Camptocheirus* sp. (Coleoptera: Curculionidae), from gall on *Cinnamomum cinnamomifolium*, K. Nishida. Deposited in USNM.

Paratypes.—COSTA RICA: two females, three males, same data as holotype. One male deposited in USNM. Two females and two males deposited in INBIO.

Distribution.—Known only from type locality in Costa Rica.

Biology.—Idiobiont ectoparasitoid of gall forming *Camptocheirus* sp. (Coleoptera: Curculionidae) on *Cinnamomum cinnamomifolium*.

Host distribution.—Costa Rica; recorded from Central Valley of Heredia (Suarez, 1992) and San José province.

Plant distribution.—*Cinnamomum cinnamomifolium*, formerly known as *Phoebe cinnamomifolia*, commonly occurs from elevations around 600 m up to about 1500 m in both the Pacific and the Atlantic slopes in Costa Rica. This plant species ranges from southern Mexico through Central America and into South America (Burger and van der Werff 1990).

Comments.—This species differs from *Compsobraconoides robustus* Quicke in having a black head, yellow clypeus, labrum,

mandibles, yellow base of first flagellomere, front and middle legs with yellow trochanters (Quicke and Sharkey 1989). It differs from *Compsobraconoides albispina* (Cameron) in having the second metasomal suture strongly arched medially, the head uniformly black, fore- and mid-tibiae yellow at basal ends rather than uniformly piceous, and hind femora entirely honey yellow rather than the apical 0.1 piceous (D. Quicke, personal communication). The host (*Camptocheirus* sp.) is a new species currently being worked on by C. H. Lyal and K. Nishida.

Etymology.—Named after host plant on which this species was found feeding on *Camptocheirus*.

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Ecology and Nesting Behavior of *Bombus atratus* Franklin in Andean Highlands (Hymenoptera: Apidae)

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Abstract.—The neotropical bumble bee *Bombus* (*Fervidobombus*) *atratus* Franklin is widely distributed in South America ranging from tropical and subtropical lowlands to high altitudes in the Andes. Most of its biology is known from studies conducted in Brazilian lowland forests and almost nothing is known from other areas, especially at high altitudes. Here we provide data on the nest architecture, brood development, worker behavior, seasonal cycle and associated organisms from seven colonies of *B. atratus* observed above 2000 m of altitude in Colombia and Ecuador. Then, we compare them with those data from Brazil. All colonies found were located above the ground, in disturbed areas. Most of the nests either lacked a defined entrance or had a single entrance; a single nest had five entrances, one of them more active than the others. Nests had from 1 to 8 active queens and up to 80 workers indicating monogynous and polygynous cycles as reported from the lowlands. Nests initially lacked an involucrum covering the brood but eventually developed an irregular involucrum of wax mixed with cardboard and carcasses of *B. atratus* and their associated beetles (*Antherophagus* sp., Cryptophagidae). Bees also built pollen pockets attached to larval clusters for feeding larvae. The average developmental time from egg to adult (29.6 days) and the percentage of cells with two pollen pockets (63.6%) were significantly greater than those previously reported. The maximum pocket diameter was significantly smaller, about half of the size, than those diameters observed in lowland colonies. The ecological significance of such reduction in size is still unclear but could explain the higher frequency of cells with two pockets in our colony. Nests maintained an internal nest temperature about 12°C warmer than external environmental temperature. Several workers were observed constantly scraping and cutting litter on top of one of the nests. Previously this behavior had only been known in *Bombus* (*Fervidobombus*) *transversalis* (Oliver), a closely related Amazonian species. As in the lowlands, *B. atratus* colonies at high altitudes seem to be active year-round. The beetle *Antherophagus* sp. was found in two of the seven colonies observed. They are probably scavengers, but nothing is certainly known about their role within tropical *Bombus* colonies.

Resumen.—El abejorro neotropical *Bombus* (*Fervidobombus*) *atratus* Franklin está ampliamente distribuido en Sur América, encontrándose desde las tierras bajas tropicales y subtropicales hasta las grandes altitudes en los Andes. Gran parte de su biología es conocida de estudios realizados en las tierras bajas brasileras y casi nada se conoce de otras áreas, especialmente a grandes alturas. Aquí proporcionamos datos sobre la arquitectura de los nidos, ciclo de desarrollo, comportamiento de las obreras, ciclo estacional y organismos asociados de siete colonias observadas a más de 2000 m de altura en Colombia y Ecuador. Luego, nuestros datos son comparados con los datos de Brasil. Todas las colonias encontradas estaban sobre el suelo, en áreas perturbadas. La mayoría de los nidos carecían de una entrada definida o presentaban una sola entrada; un solo nido tenía 5 entradas, una de las cuales era más activa que las otras. Los nidos tenían de una a ocho reinas

activas y hasta 80 obreras indicando estados monoginicos y poliginicos como ha sido registrado en las tierras bajas. Los nidos carecían de un involucro de cera cubriendo la cría, pero eventualmente desarrollaron un involucro irregular mezclado con cartón y cadáveres de abejas y los escarabajos asociados (*Antherophagus* sp., Cryptophagidae). Las abejas construyeron bolsillos de polen pegados a los grupos de larvas para suministrar el alimento. A diferencia de los registros anteriores, el promedio del tiempo total de desarrollo desde huevo a adulto (29.6 días) y el porcentaje de celdas con dos bolsillos de polen (63.6%) fueron significativamente más grandes. Sin embargo, el diámetro máximo del bolsillo de polen fue significativamente más pequeño, cerca de la mitad del tamaño, que los diámetros registrados en colonias de tierras bajas. El significado ecológico de esta reducción en tamaño es desconocido, aunque podría explicar la alta frecuencia de celdas con dos bolsillos en nuestra colonia. Los nidos mantuvieron una temperatura interna aproximadamente de 12°C mayor que la temperatura ambiental externa. Varias obreras fueron observadas constantemente raspando y cortando hojarasca en el techo de uno de los nidos; este comportamiento habia sido previamente conocido en *Bombus* (*Fervidobombus*) *transversalis* (Oliver), una especie amazónica cercanamente relacionada. Como en las tierras bajas, colonias de *B. atratus* en las grandes alturas son aparentemente activas durante todo el año. El escarabajo *Antherophagus* sp. se encontró en dos de las siete colonias observadas. Probablemente es un reciclador de materia en descomposición, pero nada es conocido con certeza sobre su papel dentro de colonias tropicales de *Bombus*.

Bumble bees (genus *Bombus*) are a diverse group of bees containing 240–250 species worldwide (Williams 1998). They are particularly diverse in temperate areas, although relatively few species are abundant in high tropical environments (Michener 2000). The neotropical bumble bee *Bombus* (*Fervidobombus*) *atratus* Franklin is widely distributed in South America ranging from warm, lowland tropical and subtropical areas to cold, high altitude ecosystems (e.g., Páramo) in the Andes up to 3400 m (Liévano et al. 1991; Chavarría 1996). Such broad geographical and altitudinal distribution suggests the ability to adapt to different pollen sources and environmental conditions. Most of what is known of its biology comes from observations made in lowland subtropical regions of Brazil (e.g., Dias 1960; Sakagami et al. 1967; Zucchi 1973; Cameron and Jost 1998), but reports from other areas, especially high altitudes, are lacking. The principal purpose of this paper is to provide data on the nest architecture, brood development and seasonality of *B. atratus* at higher elevations in the Andes of Colombia and Ecuador.

MATERIALS AND METHODS

A total of seven nests of *B. atratus* were found at two locations as follow: five nests (nests 1–5) from Facatativá (Departamento de Cundinamarca), Colombia, and two nests (nests 6 and 7) from the Botanical Garden "Reinaldo Espinosa" in Loja, Ecuador. Nests were observed from April 1996 to July 1997 (Colombia) and from February 1–19, 2001 (Ecuador). Facatativá is located at 4° 48′ 56″ N, 74° 21′ 54″ W, at 2586 m of altitude. The rainy season is bimodal with maximum rainfall in March–May and another in November (Fig. 1). The mean monthly precipitation is 689 mm and the median annual temperature is 12.4 °C (IGAC 1996). Loja is located at 2152 m and has a mean monthly precipitation of 900 mm, with most precipitation falling between December–March. The median annual temperature is 15 °C.

All Colombian nests were carefully opened and their contents recorded. Only nest 1 was captured and transferred to the Laboratorio de Investigaciones en Abejas (LABUN) of the Universidad Nacional de Colombia in Bogotá (Colombia) for closer examination. The nesting site volume was

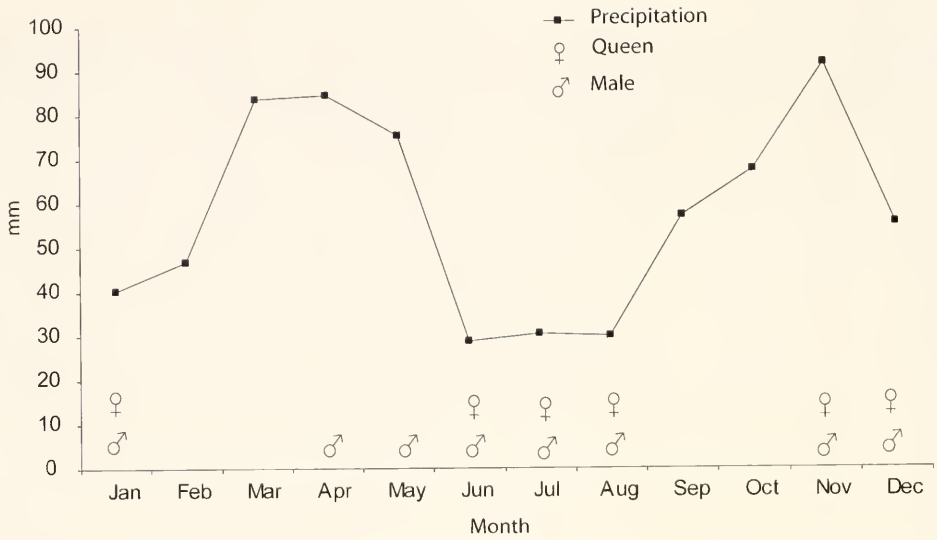

Fig. 1. Seasonal collections of queens and males of *B. atratus* in Facatativá (Colombia). Workers were found in every month.

considered as the space occupied by the brood. We multiplied the maximum and minimum diameters in cross section by the maximum height of the brood to approximate this volume. The angle of the slope of the nesting area was estimated with a compass. Observations on brood development were taken *in situ* every other day only from nest 2 over 35 days by mapping brood cells from the time of their construction to adult emergence. Cells containing larvae were easy to recognize by the presence of pollen pockets (Michener 1974), their circular shape and dark brown color derived from the pollen/wax mixture from which they are constructed. Cells containing pupae are oval-shaped and yellowish as the pollen/wax exterior is scraped off to expose the silken cocoon. The duration of the egg stage was estimated based on the construction of pollen pockets, which were generally built a day after the larva hatched. To determine the seasonal cycle of *B. atratus* in Facatativá, the insect collections of LABUN and Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (Bogotá, Colombia) were examined. Only those specimens collected between 2550 m and 3200 m of altitude from Facatativá and contiguous areas (less than 50 km^2) (e.g. Madrid, Mosquera), were included and the caste recorded. About 200 specimens were examined.

Internal nest temperature and external ambient temperature taken in shade were recorded using a digital thermometer (Reotemp® Digital TM99-A) placed directly inside the nest through one of the sides. Temperature readings started once colony disturbance died down, from 10:00 to 18:00 hrs, at intervals of 1 hr. Measurements were made only on nest 2 on January 24–26, February 1, 7–8, 1998. All measurements are given with standard errors. A t-test was used to assess significant differences between the diameter of primary and secondary pollen pockets, and between internal and external nest temperatures. All statistical analyses were performed on a personal computer using MINITAB® 14 for windows®.

Voucher specimens of *B. atratus* and associated organisms are deposited in the LABUN collection (G. Nates-Parra) and Museo Nacional de Historia Natural,

Table 1. *Bombus atratus* nests observed in Facatativá, Colombia. A = volume of nesting area (cm^3); B = number of egg cells; C = number of larval clusters; D = number of pupae; E = total number of cells; † = number of queens; w = number of workers; m = number of males. (−) = data not recorded.

Nest	Location	A	B	C	D	E	†	w	m	Observation dates
1	Pasture	—	—	—	—	598	8	63	0	Apr 27–May 22 1996
2	Eucalyptus forest	11250	15	20	70	105	1	80	0	Jun 30–Aug 4 1996
3	Eucalyptus forest	7163	4	11	10	25	2	7	3	Jan 31–Feb 6 1997
4	Pasture	3300	3	2	12	17	8	20	0	Feb 8–29 1997
5	Eucalyptus forest	1300	9	2	26	37	1	8	0	Jul 3–30 1997

Universidad Nacional Mayor de San Marcos, Lima, Perú (G. Lamas). A videotape of the nest site and instances of worker behavior on top of nest 7 in Ecuador is available from CR.

RESULTS

Nest Site and Nest Architecture

All colonies found were located above the ground. Nests in Colombia were constructed within dense bunches of grass (~40 cm height), in open, highly disturbed areas such as grazing pastures for cows and horses with scattered exotic trees such as *Eucalyptus* (Myrtaceae) and *Pinus* (Pinaceae). Nests were situated on flat ground or slopes inclined at angles of 20–30°. Nests 2, 3 and 5 were found inside *Eucalyptus* plantations; the first two were 3 m apart and nest 5 was about 420 m away from the others. Nests 1 and 4 were in a contiguous pasture area about 80 m from nest 5. Both nests 6 and 7 from Loja were found in shaded areas of the botanical garden, among *Pinus* trees, with their entrances facing west. Bees used grass as the main construction nest material mixed with dry *Eucalyputus* leaves or, in the case of nests 6 and 7, needles of *Pinus*. Three nests had a single nest entrance (about 2 cm in diameter, $n = 2$) that consisted of an irregular hole in the roof of the nest. One nest (nest 7) had five entrances, one of them more active than others and subject to modification in shape by workers over time. The remaining nests did not have a well-defined nest entrance. All nests lacked a waxen envelope (involucrum) covering the brood. However, during the first days of observations on nest 2, it developed a weak waxen involucrum mixed with small pieces of cardboard and carcasses of *B. atratus* and beetles (*Antherophagus* sp., Cryptophagidae), that eventually covered almost the entire brood. Nests approximated a circular shape with a diameter that ranged from 10–30 cm ($X = 20$ cm, $\pm$ 1.7, $n = 12$), height from 10–18 cm ($X = 13.3$ cm, $\pm$ 1.3, $n = 6$), and an average volume of 5753 cm^3 (Table 1).

Brood Development

The brood comb in all examined nests was located in a slight depression in the ground (4–5 cm deep) and, as previously recorded for *B. atratus* and various other bumble bee species, active brood cells were built on top of old, decayed cocoons, thus resulting in an upward expansion of the brood (Sakagami et al. 1967; Taylor and Cameron 2003). Egg cells were on average 5.2 mm in diameter ($\pm$ 0.1, $n = 26$) and contained from 4 to 15 eggs ($X = 9.4$ $\pm$ 1.1, $n = 8$). Individual eggs were 3.8–4 mm in length and were piled horizontally, one over the other, or sometimes were vertical at right angles to the cell axis. The egg cells were built at a rate of 1.5 cells per day. Twenty-six of 50 (52%) cells observed from first stages of construction did not reach adult emergence; 19 were destroyed by workers at the egg cell stage and 7 at the pupa stage, after the brood died. The cause of death is unknown.

Pollen pockets were constructed and attached to larval clusters for feeding larvae,

Table 2. Comparative aspects of the nesting biology of *B. atratus* from lowlands [data from Sakagami *et al.* (1967)] and high altitudes (This study). * = data from Laverty and Plowright (1985). § = duration in days, range is given in parenthesis followed by its standard error.

Biological Aspect	Lowland	Highlands
§ Duration eggs	6	6.8 (5–11) ± 0.4, n = 25
§ Larval stage	12–13	10.9 (8–14) ± 0.3, n = 21
§ Pupa	8–12	12.8 (10–15) ± 0.3, n = 15
§ Total time egg-adult	*26.7 (24–34) ± 0.8, n = 7	29.6 (28–31) ± 0.3, n = 15
Pollen pockets/cell	1–3	1 and 2
Freq. one pocket	74 %	36.4 %
Freq. two pockets	21 %	63.6 %
Freq. three pockets	5.3 %	0
Pocket diameter (mm)	7.3 (4–10) ± 0.1, n = 177	3.7 (3–6) ± 0.1, n = 80

as previously noted in *B. atratus* and other species of the subgenus *Fervidobombus* (Sakagami et al. 1967; Sakagami 1976; Taylor and Cameron 2003). These pockets were usually made one day after the larvae hatched, generally between the sixth and seventh day after the queen laid the eggs, and remained for a period of 6.5 days on average (n = 22 cells). Eight and 10 larval cells had one and two pockets, respectively, throughout the feeding period; however, bees built a second pocket for four of the eight cells several days after the first one was built and in one case, bees destroyed one of the two pockets initially built. The maximum diameter of the secondary pockets ranged from 3 to 6 mm (X = 3.7 ± 0.1, n = 80) and there was no statistical difference in the mean diameter between the two pockets (*t-value* = 0.53, $P > 0.01$).

The total developmental time from egg to adult observed in our study is within the range found by Sakagami et al. (1967) and Laverty and Plowright (1985) for lowland *B. atratus* colonies (Table 2). However, the average value for the developmental time was significantly longer in our study than that reported by Laverty and Plowright (1985) (*t-value* = 4.53, $P < 0.01$).

Nest Thermoregulation

Internal nest temperatures ranged from 23.8–29.9 °C (X = 27.2 °C ± 0.3, n = 35) and remained about 11.5 °C warmer than external ambient temperatures (X = 15.7 °C ± 0.9, range = 5–22.5 °C, n = 26). Internal nest temperature was significantly higher than external ambient temperature ($P < 0.01$, t-test).

Worker Behavior

An approximate number of nine workers from nest 7 were observed manipulating litter persistently on top of the nest. These workers actively walked around, constantly scraping litter with their mandibles and pushing the litter beneath their body with the help of the forelegs, as reported for *Bombus* (*Fervidobombus*) *transversalis* (Oliver) (Cameron et al. 1999). Small pieces of litter were simply moved out of the way whereas larger pieces, such as large leaves mainly found at the margins of the nest area, were cut into small pieces (≪2 cm). During the observation period, bees were not seen bringing pieces of litter in or out of the nest. The specificity of these workers to work on top on the nest could not be established since they were not individually marked. This behavior was not noted on the nearby nest 6 in Ecuador or on any of the Colombian nests.

Colony Life Cycle and Seasonality

The number of queens and workers per colony in the Colombian nests at the times they were found ranged from 1–8 queens and from 8–80 workers. Males were only

present in a single small colony (Table 1). The colony size of the Ecuadorian nests could not be established; however, a total of four dead queens in different degrees of decomposition were found outside the entrance of nest 7 upon discovery. One of the queens was partially buried in the ground. Later on February 19, at the same nest, other two dead queens and three workers were found outside the nest entrance; one of the two queens lacked wings. Males were collected foraging on flowers around the nesting area in Ecuador.

Appraisal of museum specimens revealed that workers of *B. atratus* had been collected in every month of the year from Facatativá and surrounding areas, whereas queens and males were collected only during periods of the year with less precipitation (Fig. 1).

Associated Organisms

Beetles of the genus *Antherophagus* were found inside the old comb and debris of the nest, at the bottom of the comb in two of the five observed colonies from Facatativá. They were more active and frequently seen in upper areas of the nest where they tried to reach foragers during the terminal phase of the colony. They were also regularly seen attached to the hind legs of workers at flowers.

DISCUSSION

All nests were found on the ground and covered with vegetable material as previously reported for *B. atratus* at lower altitudes. None of the dissected nests (nests 1–5) had a waxen involucrum covering the brood when found; however, as reported by Sakagami et al. (1967), this species can eventually develop a thin layer of waxen involucrum mixed with dead leaves and dead insect parts. The use of man-made materials to build the involucrum such as cardboard is reported for the first time. The origin of the cardboard is unknown and no bees were observed bringing or collecting such material; nonetheless, it is likely that the cardboard was present at the nest site prior to the establishment of the colony since most bumble bees modify the materials available at the site of nest construction (Michener 1974). The construction of the involucrum by nest 2 was likely a response to mechanical disturbance when taking observations of the nest, but may also be a strategy to protect the nest during inclement weather. Further observations are required to determine this.

The observation of workers manipulating and cutting pieces of litter on top of the nest in Ecuador is very similar to behavior otherwise known only in the Amazonian bumble bee *Bombus transversalis* (Cameron et al. 1999), but it is not surprising in a phylogenetic sense. In fact, molecular and morphological analyses suggest that *B. atratus* comprises a clade with *B. transversalis* and *B.* (*Fervidobombus*) *pullatus* Franklin (Cameron and Williams 2003). The latter two species are the only primarily tropical rain forest species of *Fervidobombus*. The fact that leaf-cutting behavior was seen only at one of the Ecuadorian nests, and at none of the Colombian nests, suggests variability in the expression of this behavior. More observations are necessary to determine the ontogenetic or seasonal, if any, components that may influence leaf-cutting.

Bombus atratus is perhaps the only neotropical bumble bee that exhibits a broad plasticity in nest site selection, ranging from cavities constructed below ground (Cameron and Jost 1998) to aerial nests built in trees (Dias 1960). It is found in forest, savanna, and highly disturbed grassland, as reported in this note. This flexibility in nesting habit, as well as the ability to use exotic pollen sources (Liévano and Ospina 1984; Gonzalez unpublished data), are likely important factors enabling this species to inhabit diverse environments.

Bombus colonies from temperate areas have a typical annual cycle and one queen

per colony. Tropical lowland colonies of *B. atratus* are considered perennial, switching between polygynous and monogynous cycles (e.g., Moure and Sakagami 1962; Zucchi 1973; Cameron and Jost 1998). The colonies observed in our study had from one to several queens. Although we have no data, it is possible that more than one of these queens was reproductive inside the nest. The dead queens found outside the entrance of nest 7 hints at the possibility that this nest had recently gone through a polygynous phase that led to the death of all but one queen (Cameron and Jost 1998). Additional observations (R. Ospina pers. comm.) of multi-female nests of *B. atratus* in the Andes corroborate such cycles of polygyny and monogyny. Queens and probably males may be active outside of their nests throughout the year even though specimens of these castes were not seen in collections from Facatativá and vicinity during the rainy periods. Queens and males have been collected during March and September–October in less seasonal areas than Facatativá at similar altitudes (e.g., La Calera; Gonzalez pers. obs.) and therefore are present during every month of the year at these altitudes. Thus it may be possible for *B. atratus* to initiate new colonies at any time of year, as noted for *Bombus* (*Pyrobombus*) *ephippiatus* Say from the highlands of Costa Rica (Laverty and Plowright 1985).

In general, our observations on the brood development of nest 2 agree with those of Sakagami et al. (1967) from a single captive colony. The most striking differences between the studies, however, are in the frequency of the number of pollen pockets per cell, pocket diameter and the total developmental time. Although our sample size was about half the number of cells observed by Sakagami et al. (1967), our nest had, in proportion, more cells with two pollen pockets. The maximum diameter of the pollen pockets observed in our colony was significantly different, about half the diameter of those observed by Sakagami et al. (1967) (*t-value* = 19.53, $P < 0.01$; Table 2). In addition, their colony had cells with three pollen pockets. The ecological significance of such reduction of the pocket size in our colony is unclear but could explain the higher frequency of cells with two pockets. Additional observations on different colonies are needed to understand the significance of the pollen pocket numbers.

The longer average value for the developmental time from egg to adult observed in our study than that reported by Laverty and Plowright (1985) was somewhat expected. Low temperatures at high altitudes might delay development, though, as we show here, *B. atratus* colonies are able to keep their internal nest temperature higher than external ambient temperature; however, they would have to invest more energy to do this at cooler temperatures. Our data support other observations (Laverty and Plowright 1985) that brood development times in neotropical species are on average longer than those for temperate bumble bees.

Although tropical high altitude environments are relatively cooler year-round, they experience large daily changes in weather conditions, which influence diurnal flight activity. Foraging under such conditions may be restricted to taxa such as bumble bees that can effectively regulate body temperature (Heinrich 1979; Bishop and Armbruster 1999). Our data show that, as in other bumble bee species (e.g., *B. transversalis*, Taylor and Cameron 2003), workers in *B. atratus* nests can maintain a stable nest temperature warmer than ambient, presumably by incubating the brood cells through heat produced by muscular contractions (Heinrich 1979). Regulation of body and nest temperature can be particularly important and even critical for bees at high altitudes where air temperature can quickly change from several degrees below zero up to 23 °C. For instance, small sleeping aggregations of males of solitary Andean bees such as

Thygater aethiops Smith (Apidae, Eucerini) are occasionally found dead, frozen and hanging on leaves when temperatures reach several degrees Celsius below zero (Gonzalez and Engel in press). Thus, if the maintenance of internal nest temperature in *B. atratus* depends on colony size, larger colonies are likely to be favored over smaller colonies in such Andean environments. Nonetheless, our colonies were smaller than those reported in lowland environments.

The association between *Antherophagus* beetles and *B. atratus* was first noted by Roubik and Wheeler (1982) from a colony kept in captivity in Bogotá, Colombia at 2600 m of altitude. Species of *Antherophagus* have also been reported from neotropical bumble bees such as *B. ephippiatus* from Costa Rica (Chavarría 1994). They are probably scavengers, given that they are found within the nest debris in healthy colonies, but besides these reports nothing is known about their role within tropical *Bombus* colonies.

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A New Species of *Quadrastichus* (Hymenoptera: Eulophidae): A Gall-inducing Pest on *Erythrina* (Fabaceae)

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Abstract.—*Quadrastichus erythrinae* Kim sp.n. is described from Singapore, Mauritius and Réunion. This species forms galls on the leaves, stems, petioles and young shoots of *Erythrina variegata* and *E. fusca* in Singapore, on the leaves of *E. indica* in Mauritius, and on *Erythrina* sp. in Réunion. It can cause extensive damage to the trees.

Key words.—Hymenoptera, Eulophidae, *Quadrastichus*, phytophagous, gall inducer, Singapore, Mauritius, *Erythrina*, Fabaceae

Species of Eulophidae are mainly parasitoids, but secondary phytophagy in the form of gall induction has arisen on many occasions (Bouček 1988; La Salle 1994; Headrick et al. 1995; Mendel et al. 2004; La Salle 2004). Gall-inducing Eulophidae generally belong to two groups: Ophelimini is an Australian lineage which consists mainly of gall inducers on eucalypts, but perhaps also on some other myrtaceous hosts (Bouček 1988; La Salle 2004); and Tetrastichinae includes several instances of gall induction, but it is questionable that these represent a single evolutionary event (La Salle 2004). Genera of Tetrastichinae where gall induction is known to occur include *Quadrastichodella*, *Oncastichus*, *Epichrysocharis*, *Aprostocetus*, *Paragaleopsomyia*, *Ceratoneura*, *'Exurus'*, and *Leptocybe* (La Salle 2004; Mendel et al. 2004).

Several species of tetrastichine gall inducers have become invasive pests, particularly in the last decade, these include: *Quadrastichodella nova* Girault (Flock 1957, as *Flockiella eucalypti*; Timberlake 1957, as *Flockiella eucalypti*; Bouček 1988); *Oncastichus goughi* Headrick & LaSalle (Gough 1988; Redak and Bethke 1995; Headrick et al. 1995); *Epichrysocharis burwelli* Schauff (Schauff and Garrison 2000); and *Leptocybe invasa* Fisher & La Salle (Mendel et al. 2004). *Quadrastichus erythrinae* Kim sp.n. has recently achieved pest status in Singapore, Mauritius and Réunion. *Erythrina* trees have been grown in these areas for decades, and this species has never been recorded from them. Although its exact origin remains unknown, it is likely to represent another example of an invasive pest species.

There are approximately 110 species of *Erythrina* around the world, mostly found in tropical regions (Mabberly 1987). Their beautiful red flowers have earned them the common name of coral trees, and made them a popular tree to be used in landscaping in many tropical regions.

Recently, a eulophid species was found from galls on *Erythrina* in Singapore and sent to one of us [JL]; at about the same time galls were found in Mauritius and Réunion, with wasps being sent to another of us [GD]. Comparison of the two samples showed that there was a single, widespread species involved. This wasp can

cause severe damage to *Erythrina* trees, and has become a nuisance in these countries.

Records of gall-inducing wasps on *Erythrina* are not extensive. Annecke & Moran (1982) reported on *Erythrina* galls in South Africa. Five species of chalcidoid wasps were reared from these galls, the most common being a Eulophidae sp. and a *Eurytoma* sp. (Eurytomidae). At that time, the *Eurytoma* was suspected as being the gall inducer. Recent examination of the material (by Dr. G.L. Prinsloo) has shown that there are two eulophid species present, but neither of them are the same as *Q. erythrinae*. Because this species was found on Réunion and Mauritius, one of us [GD] compared this species with all species described by Risbec from Madagascar; however, it did not agree with any previously named species.

Quadrastichus erythrinae Kim represents the first record of a gall inducer in the genus *Quadrastichus*. Species of *Quadrastichus* have a variety of biologies: many are parasitoids of gall-inducing hosts, such as Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera); others are parasitoids of Buprestidae and Curculionidae (Coleoptera), or Agromyzidae and Tephritidae (Diptera); *Q. sajoi* (Szelényi) larvae are predators of eriophyid mites within galls (Graham 1991, La Salle 1994, Hansson and La Salle 1996).

Terminology used in this paper is taken from Gibson (1997) and Graham (1987); OOL, ocell–ocular distance; POL, postocellar distance; MPS, multiporous plate sensilla.

Acronyms used in the text are as follows. ANIC, Australian National Insect Collection, CSIRO Entomology, Canberra, Australia; BMNH, The Natural History Museum, London, UK; CIRAD, Centre de Coopération Internationale en Recherche Agronomique pour le Développement; CNC, Canadian National Insect Collection, Ottawa, Ontario, Canada; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; PPRI, Biosystematics Division, Plant Protection Research Institute, Pretoria, South Africa; QMB, Queensland Museum, Brisbane, Australia; USNM, United States National Museum of Natural History, Washington, D.C., USA.

SYSTEMATICS

Quadrastichus erythrinae Kim, sp.n.

(Figs 1–10)

Types. Holotype ♀: SINGAPORE, 02.vi.2003, He Liansheng, reared from galls on *Erythrina fusca* (ANIC).

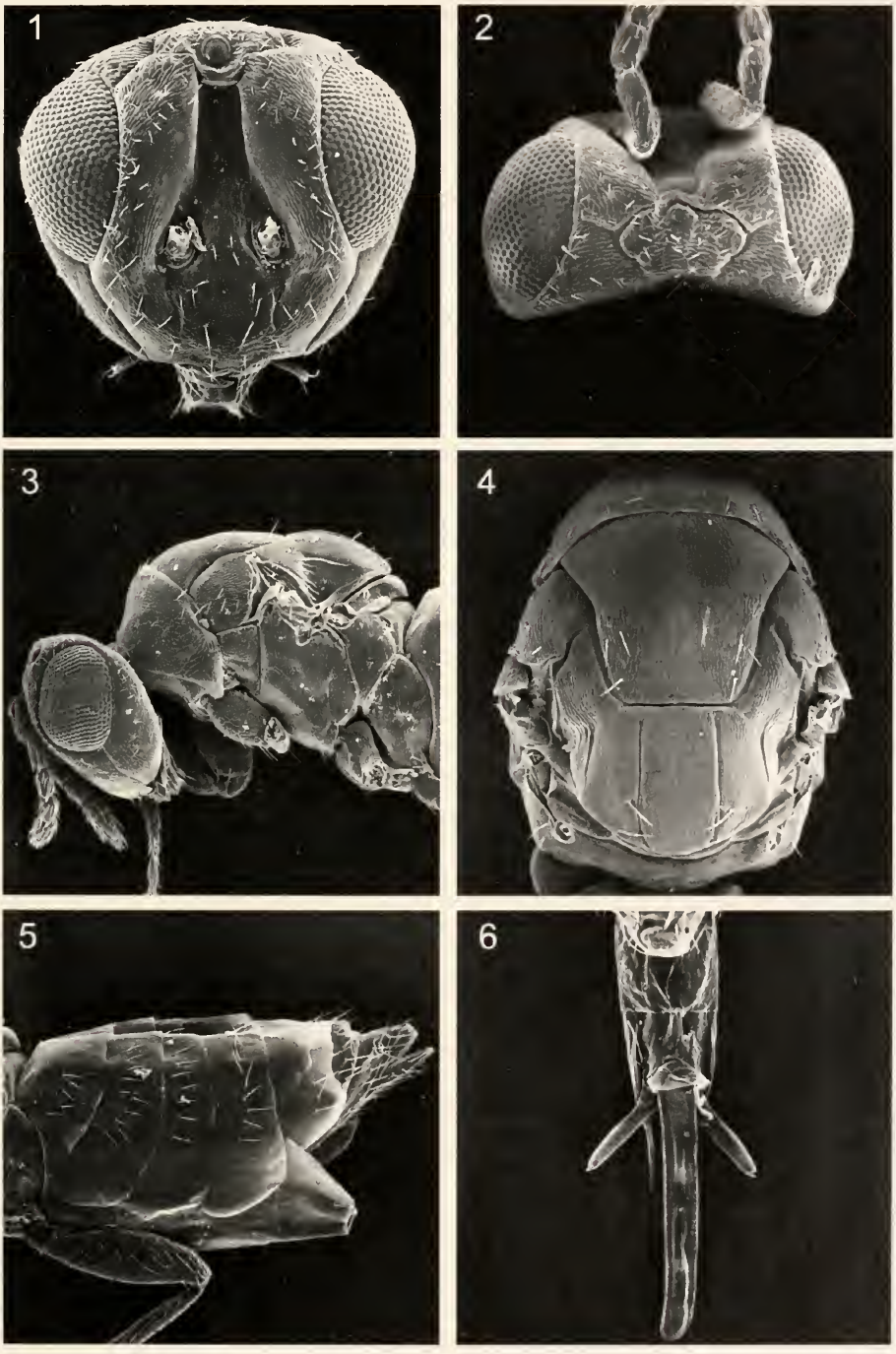
Paratypes: 63♀, 118♂, Same data as Holotype (28♀, 83♂ ANIC; 5♀, 5♂ each: BMNH, CIRAD, CNC, MZB, PPRI, QMB, USNM).

Non-type material: MAURITIUS: Bras d'Eau, 04.iv.2003, D. Ramkhelawon, vii.03, ex. *Erythrina indica* leaves (12♀, 14♂, ANIC); Quatre Bornes, 17.vii.2003, (S. Permalloo), ex. leaf galls on *Erythrina indica* (3♀, 5♂, ANIC). LA RÉUNION: Saint-Pierre, Bassin Plat, 06.xii.2000, G. Delvare & A. Franck, ex. galls on *Erythina* sp. (33♀, 38♂ CIRAD); Saint-Benoît, 24.ii.2003, S. Quilici, ex. galls on *Erythina* sp., Ref. N° RQ 4611 & Cirad 18009 (21♀, 11♂ CIRAD).

Description

Female Length 1.45–1.6 mm. Dark brown with yellow markings. Head yellow, except gena posteriorly brown. Antenna pale brown except scape posteriorly pale. Pronotum dark brown. The mid lobe of mesoscutum with a "V" shaped or inverted triangular dark brown area from anterior margin, the remainder yellow. Scapula yellow. Scutellum, axilla and dorsellum brown to light brown. Propodeum dark brown. Gaster brown. Fore and hind coxae brown. Mid coxa almost pale. Femora mostly brown to light brown. Specimens from Mauritius are generally darker than those from Singapore.

Head (Figs 1–2). Ocellar triangle surrounded by groove; transverse groove ex-



Figs. 1–6. *Quadrastichus erythrinae* sp. n.—1. Head, frontal view; 2. Head, dorsal view; 3. Head and thorax, lateral view; 4. Mesosoma, dorsal view; 5. Gaster, lateral view; 6. ♂Genitalia, dorsal view.

tending from lateral ocellus to eye. POL 1.6–2.0 times longer than OOL. Frons with broad median area, but without median carina. Toruli situated at level of lower eye margin. Shallow groove present beneath torulus, extending slightly over half the distance from torulus to clypeal margin. Gena slightly swollen and malar sulcus only slightly curved, without triangular fovea below eyes. Clypeal margin bidentate.

Antenna (Fig. 7) with one large anellus. All funicular segments 1.3–1.6 times longer than wide and each segment approximately equal in length and width to the others. However, under the microscope with slide-mounted antenna, each successive segment appears slightly wider than previous one. Sensilla (MPS) slightly shorter than length of funicular segment, each sensilla reaching to the next funicular segment; 1–2 sensillae visible on each segment in lateral view. Scape not extending above the vertex.

Mesosoma (Figs 3–4). Median line on the mid lobe of mesoscutum very weak to absent but usually at least indicated in certain angles and light; if indicated, it can be seen superficially only in posterior half. Mid lobe of mesoscutum with 3 to 5 short adnotaular setae. Scutellum with distinct submedian lines and sublateral lines; 2 pairs of setae on scutellum (occasionally with an additional seta), anterior seta situated well behind midlength of scutellum. Precoxal suture distinct and extending about 0.7 length of mesopleuron. Propodeal spiracle relatively large, whole rim exposed. Propodeum without distinct median carina or paraspiracular carina. Propodeal callus with 2 setae.

Wing (Figs 9–10). Submarginal vein with 1 seta, situated slightly basal to the middle. Costal cell without setae. Postmarginal vein almost rudimentary; less than 0.3 length of stigmal vein. Costal cell: marginal vein: stigmal vein: postmarginal vein = 3.9–4.1: 2.8–3.1: 1.0: 0.1–0.3. Cubital line of setae not extending all the way to basal vein, leaving the speculum partially open behind; the speculum small.

Gaster (Fig. 5). Slightly longer than the head plus mesosoma. Hypopygium extending 0.8–0.9 the length of gaster and reaching up to the posterior margin of G6. Ovipositor sheath not protruding, short in dorsal view. Cercus with 3 setae, the longest one slightly curved and about 1.3 as long as the others, which are subequal in length.

Male. Length 1.0–1.15 mm. Pale coloration white to pale yellow as opposed to yellow in female. Head and antenna pale. Pronotum dark brown (but in lateral view, only upper half dark brown; lower half yellow to white). Scutellum and dorsellum pale brown. Axilla pale. Propodeum dark brown. Gaster in anterior half pale; remainder dark brown. Legs all pale.

Antenna (Fig. 8) with 4 funicular segments; without the whorl of setae; F1 distinctly shorter than the other segments and slightly transverse; about 1.4 wider than long. Ventral plaque extending 0.4–0.5 length of scape and placed in apical half.

Gaster shorter than female. Genitalia (Fig. 6) elongate, with digitus about 0.4 length of the long, exserted aedagus. [Dorsally exposed parts of the genitalia were measured.]

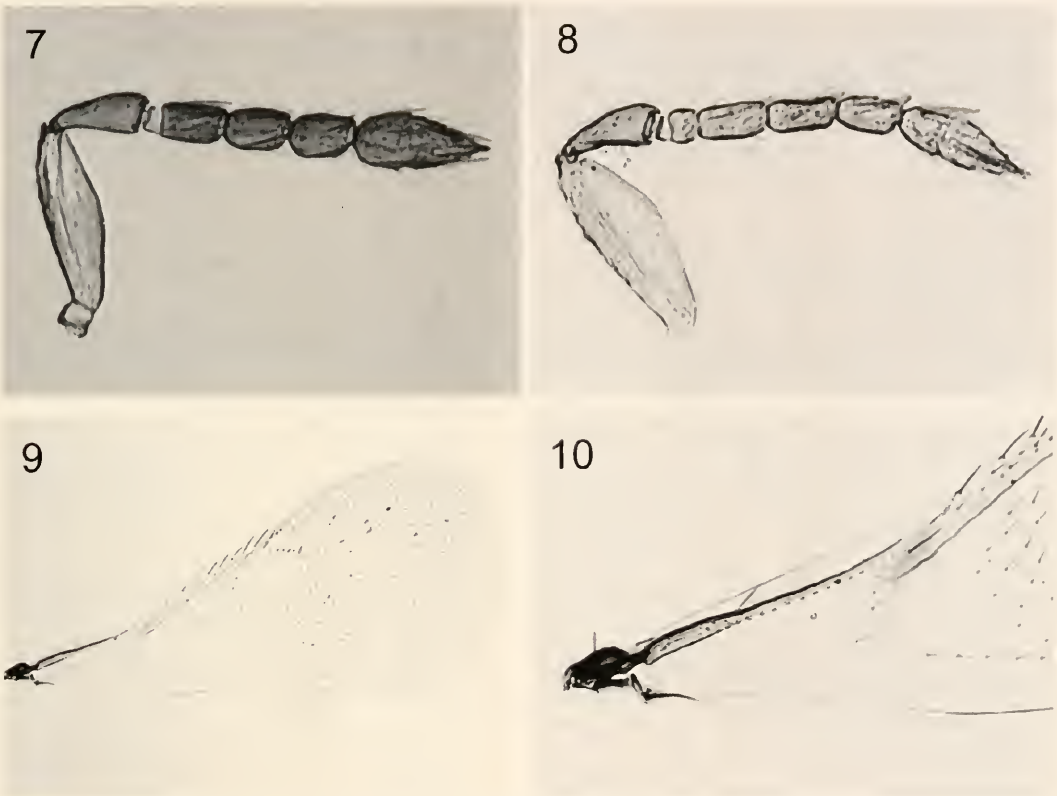
Etymology. The specific name *erythrinae* comes from the genus name of the host plant.

Biology. Reared from galls on *Erythrina variegata* L., *E. fusca* Lour. (=*E. glauca* Willd.) and *E. indica* L. (Figs 11–12). Inside the leaf galls there is usually only one wasp per cell, while in the swollen tissues of shoots, twigs and petioles more than five individuals were observed.

Distribution. Singapore, Mauritius, Réunion. It is not known if this wasp is native to one of these regions or not.

Discussion

This species fits the definition of *Quadrastichus* offered by Graham (1991): SMV



Figs. 7–10. *Quadrastichus erythrinae* sp. n.—7. Antenna, ♀; 8. Antenna, ♂; 9. Forewing; 10. Submarginal vein.

Figs. 11–12. Galls on stems, petioles, and young shoots of *Erythrina* induced by *Quadrastichus erythrinae*.

with 1 dorsal seta, antenna with all funicular segments longer than wide and with 1–3 anelli in female and gaster longer than the head plus mesosoma. However, the species is distinct from all other *Quadrastichus* on the basis of the long hypopygium.

The only key to species of *Quadrastichus* of any region is Graham (1991) for European species. In this key, this species would run to the *anysis*-group of *Q. anysis* (Walker), *Q. citrinus* (Thomson) and *Q. xanthosoma* (Graham) as follows: body black and yellow as opposed to metallic and without yellow markings; frons with median area but without median carina; gena slightly swollen, malar sulcus only slightly curved, malar sulcus without a large subtriangular fovea just beneath eye.

However, *Quadrastichus erythrinae* differs from the *anysis*-group because: clypeal margin bidentate, scape not exeeding above the vertex, apex of hypopygium extending distinctly beyond middle of gaster. Males of the *anysis*-group have whorls of long setae on the funicular segments (Graham, 1991; Reina & La Salle, 2004), however these are absent in *Q. erythrinae*. Additionally, the *anysis*-group appears to be restricted to leafminer hosts.

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Hooked Hairs and Not So Narrow Tubes: Two New Species of *Colletes* Latreille from Texas (Hymenoptera: Apoidea: Colletidae)

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Abstract.—Two new species, ***Colletes bumeliae*** **Neff** and ***Colletes inuncantipedis*** **Neff,** are described from central Texas, U.S.A. Both have arrays of specialized, recurved setae on their foretarsi which are used to extract pollen from flowers of *Sideroxylon lanuginosum* (A. Michaux) Pennington (Sapotaceae), their primary floral host. Nests and provisioning behavior are described for *C. inuncantipedis.*

Colletes is a nearly cosmopolitan genus of bees consisting of more than 440 species (Michener 2000, Kuhlmann 2003). Roughly 100 species have been recorded from North and Central America, making *Colletes* one of the larger genera of American bees (Michener et al. 1994). While many species of *Colletes* are believed to be oligolectic (Stephen 1954, Moldenke 1979, Mader 1999, Müller and Kuhlmann 2003) very little has been reported on either their pollen collecting behavior or any morphological features which may enhance pollen harvesting by these bees. This is not particularly surprising since most North American *Colletes* lack obvious specializations for pollen harvesting beyond the usual branched body hairs and tarsal and tibial brushes of simple setae (Thorp 1979). The few exceptions include the sternal setal brushes of females of some members of the *consors* group of Stephen (1954) used for pollen collection during vibratile pollen harvesting from the flowers of *Chamaesaracha, Quincula* and *Physalis* (all Solanaceae) (Stephen 1954, J. L. Neff pers. obs.), and arrays of hooked setae on the clypeus and frons of an undescribed Mexican species that aid in collecting pollen from the nototribic anthers of flowers of the Lamiaceae (G. Dieringer, pers. com.). In addition, females of some Mesoamerican *Colletes* (including *C. isthmicus* Swenk and *C. mexicanus* Cresson) have a metasomal scopa comprised of setae with hooked apices (Griswold et al. 1995). I here add to this short list by describing two distinctive new species from central Texas. Females of both species have unusual arrays of hooked setae on their foretarsi which are employed in the collection of pollen from the partially hidden anthers of flowers of *Sideroxylon* Linnaeus (Sapotaceae).

MATERIALS AND METHODS

Morphological nomenclature follows Michener (2000) with the addition of the terms clypeal apicomedial and apicolateral fovea for the sensillae bearing fovea on the apical margin of the clypeus. Definitions for abbreviations and measurements are as follows: UIOD—upper interocular distance (minimal distance between compound eyes on upper part of face); LIOD—lower interocular distance (minimal distance between compound eyes on lower portion of face); MIOD—maximal interocular distance (maximal distance between compound eyes); OCD—ocellar diameter; PW—puncture width; T1, T2, T3 . . .—Metasomal Tergum 1, Tergum 2, Ter-

gum 3 . . . ; S1, S2, S3 . . .—Metasomal Sternum 1, Sternum 2, Sternum 3 . . . ; BL—body length (length front of vertex to posterior margin of T2); FW—forewing length (measured from base of the radial cell to apex of marginal cell); HW—head width (maximal width in frontal view). Acronyms used include: BFL—Brackenridge Field Laboratory of The University of Texas, Austin, Texas; SEMC—Natural History Museum, University of Kansas, Lawrence, Kansas; TAMU—Entomology Collection of Texas A & M University, College Station, Texas and J.L.N.—J.L.Neff.

The lengths of the foretarsi (and femora and tibiae) of female *Colletes bumeliae* and *C. inuncantipedis* were compared with those of females lacking the specialized hooked hairs. Lengths were adjusted for size by dividing the appropriate leg length by head width. Adjusted tarsal and other leg length measures did not differ between *C. bumeliae* and *C. inuncantipedis* so they were combined for further analyses. For comparative purposes, I also used two measures of forewing length as the divisor: as defined above and, in unworn specimens, from the base of the radial cell to the distal wing apex). Seventy-five individuals from 39 species (two or rarely one female per species), were used for the analysis (11 females were excluded due to extensive wing wear for the second wing length analysis). *Colletes* species included in the tarsal length analysis are: *C. aestivalis* Patton, *C. algarobiae* Cockerell, *C. aztekus* Cresson, *C. aridus* Stephen, *C. beamerorum* Stephen, *C. birkmanni* Swenk, *C. brevicornis* Robertson, *C. cercidii* Timberlake, *C. clypeonitens* Swenk, *C. compactus* Cresson, *C. delicatus* Metz, *C. deserticola* Timberlake, *C. eulophi* Robertson, *C. fulgidus* Swenk, *C. gilensis* Cockerell, *C. gypsicolens* Cockerell, *C. hyalinus* Provancher, *C. intermixtus* Swenk, *C. louisae* Cockerell, *C. latitarsis* Robertson, *C. mandibularis* Smith, *C. mitchelli* Stephen, *C. nigrifrons* Titus, *C. paniscus* Viereck, *C. perileucus* Cockerell, *C. prosopidis* Cockerell, *C. saritensis* Stephen, *C. scopiventer* Swenk, *C. simulans* Cresson, *C. skinneri* Viereck, *C. sleveni* Cockerell, *C. swenki* Stephen, *C. texanus* Cresson, *C. thoracicus* Smith, *C. willistoni* Robertson, *C. wilmattae* Cockerell and *C. wootoni* Cockerell.

Colletes bumeliae Neff, new species

Diagnosis.—The female of *Colletes bumeliae* is easily distinguished from all other Nearctic *Colletes*, except *C. inuncantipedis*, by the distinctive arrays of hooked hairs on its forebasitarsi. It fails at couplet 71 in the female key of Stephen (1954) due to the absence of dark hairs on the mesoscutum and scutellum; mesepisternum strongly punctate, not rugose; and absence of basal fascia on T2. The male runs to *Colletes kansensis* Stephen (couplet 71 in Stephen's key) but is readily distinguished by the shape of the 7th sternite, the punctation of T1 fine and sparse medially, and the tegulae translucent brown, not black. *Colletes bumeliae* is clearly closely related to *C. inuncantipedis*. The form of the genitalia and the metapleural prominence suggest *kansensis* may be the closest relative to these two species. Unfortunately, the female of *kansensis* is unknown.

Description.—♀. Measurements: (N = 9) BL: 7.0–8.2 mm; FW: 4.5–5.2 mm; HW 2.8–3.1 mm. ***Head***: Face 1.24–1.29 × wider than long, greatest distance between eyes exceeding eye length, inner orbits strongly convergent below and arched inward above (UIOD 1.11–1.15 × LIOD, UIOD 0.81–0.89 × MIOD). Malar space about ¼ as long as wide. Clypeus slightly produced with depressed, flattened, impunctate, apical margin; clypeal disk shining, densely, striately punctate, often with small, shining, impunctate medioapical area; punctures smaller, denser and nonstriate basally and laterally. Clypeal apicomedial fovea large and round, apicolateral fovea smaller and much weaker. Disc of supraclypeal area raised, surface dull and microstriate with sparse, moderate, punctures; punctation of lateral surfaces

smaller and much denser. Median line carinate from above supraclypeal area to median ocellus. Disc of labrum rounded, shining, impunctate, without median groove. Frons with punctures strong, dense and nearly contiguous. Facial fovea deeply impressed, broadest medially but restricted above, curving inward towards lateral ocellus; upper margin of fovea at or slightly above line between summits of eyes, upper inner margin of fovea narrowed, within 1 OCD of lateral ocellus, fovea tapering below, extending to level just above upper margin of antennal fossae; surface dull, microstriate. Vertex shining, densely, minutely punctured except shining impunctate area between lateral ocelli and facial fovea. Gena narrow, broadest below; genal width 0.5 × eye width at level of antennal insertion; punctures dense above becoming striate below and on hypostomal area. Scape slender, length 5 × apical width. Minimal length first flagellar segment short, minimal length slightly less than apical breadth. Middle antennal segments slightly longer than broad. ***Thorax***: Pronotal spine short but sharp; broad basally, abruptly narrowing to acute tip. Tegulae sparsely punctate, most punctures in apical ⅓. Mesoscutum shining, disc strongly punctate with punctures separated 1–1.5 pw on anterior ⅔, punctures much sparser on posterior ⅓, punctures finer and denser on anterior and posterior mesoscutal margins. Scutellum shining, punctures strong, similar to discal mesoscutal punctures on posterior ⅔, punctures smaller and denser on posterior margin but very sparse, nearly impunctate on anterior third. Metanotum rugose. Mesepisternum anterior to quadrately pitted episternal groove densely punctate; punctures slightly coarser than those of mesoscutum, punctures less than 1 pw apart. Mesepisternum posterior to groove with punctures decreasing in size and density posteriorly (except punctures dense along meso-metepisternal suture) with posterior most punctures <½ diameter of anterior punctures; interspaces shining; hypoepimeral area shining, sparsely punctate. Metepisternum shining, quadrately pitted; metapleural prominence small, rugose, with short, opaque, curved, carinate rim above small shining declivity. Propodeum with dorsal area shining, quadrately pitted; posterior surface of propodeal triangle shining; posterior propodeal surface outside triangle coarsely roughened, posterolateral margins of propodeum weakly carinate. Fore basitarsis broad, subrectangular (basal width 0.37 × length, fore basitarsal length 0.58 × fore tibia); hind basitarsis broad, roughly 3× as broad as long, sides subparallel. ***Abdomen***: Terga shining, with narrow impunctate margins; punctation of T1 fine and dense laterally but much sparser, nearly impunctate in medial ¼ to ⅕; discal punctation of distal terga uniformly fine and dense. Punctation of S 1–2(3) moderately dense, slightly coarser than terga, becoming finer on distal sterna, apical margins of sterna with narrowly translucent. Apex of S6 slightly depressed, surface shining with density of punctures decreasing towards apex. ***Vestiture***: Pile of face white, dense and partially obscuring surface on frons but sparse on vertex, clypeus and supraclypeal area; hairs of clypeus, short, sparse, simple and semi-appressed; 1–2 long, bent, flattened simple setae in apicomedial fovea of clypeus, 3–4 shorter branched setae in apicolateral fovea. Pile of vertex pale yellowish-white, hairs branched and relatively dense in and behind ocellar triangle but sparse and simple in ocello-ocular space; hair of upper part of gena dense with numerous short branched hairs, appressed along upper posterior margin of eye, becoming much sparser and less branched below. Pile of mesoscutum and scutellum pale, yellowish-white, hairs short with numerous long branches; dense fringe of white, branched hairs on posterior margin of pronotal lobe, pile of mesepisterna, erect and sparse, not obscuring surface; propodeal corbicula

well developed with strong dorsoposterior fringe of pale hairs, weakly delimited anteriorly with short fringe of pale branched hairs, corbicular surface with mix of appressed short hairs and erect simple hairs, latter primarily in posterolateral third. Anterior series of parallel branched femoral scopal hairs typical for genus but posterior series of radially branched hairs reduced, consisting of ca. 25. Foretarsi with abundant erect, hooked simple hairs, particularly on dorsal surface of basitarsis and apices of distal tarsal segments. Usual brushes of simple hairs of hind basitarsis also well developed on distal tarsal segments. Hair of coxae, trochanters and femora white or off-white. Hair of tibiae and tarsi white. Pile of T1 white, relatively dense anterolaterally with sparse, erect hairs anteromedially, becoming very sparse on disc, with complete apical white fascia; T2–5 with complete apical white fascia, but fascia weak on T4 and 5. Discs of T2–5 with short dark hair not obscuring surface; with sparse, pale, erect hair on lateral margins. T6 with mix of appressed long and short dark hair. S1 with erect pale branched hairs, S2–6 with sparse simple semi-appressed hairs, hairs shortest on basal portion of each sternite, becoming longer distally but not forming distinct fascia. **Color**: Black, except mandibles, tibial spurs, pretarsal claws; terga 3–6, sterna and distal tarsomeres brown; apices of T 1–4 and S 1–5 narrowly translucent brown. Tegulae translucent brown; wings hyaline, with abundant short dark hairs, veins reddish brown with pterostigma translucent reddish brown.

♂.—Measurements: (N = 10) BL, 5.1–8.2 mm; FW 4.4–5.7 mm, HW 2.5–3.2 mm. ***Head***: Face 1.24–1.44 × wider than long, greatest distance between eyes slightly greater than eye width; inner margins strongly convergent below, UIOD 1.25.1.39 × LIOD, UIOD 0.85–0.92 MIOD. Malar space 0.4 times as long as wide. Clypeus with disc raised and rounded, surface shining, punctures fine, dense and elongate medially, but much sparser laterally, almost impunctate anterolaterally, apical margin narrowly depressed. Labrum with disc evenly rounded, impunctate and shining. Supraclypeal area densely punctate, medial punctures roughly twice diameter of peripheral punctures. Supraclypeal median line carinate to just below median ocellus. Punctures of frons coarse and dense. Facial fovea relatively narrow, expanded subapically, upper portions of facial fovea strongly depressed along edge of eyes, outer margins carinate, surface of fovea dull. Punctures of vertex fine, dense with impunctate space laterad ocelli. Gena shining, finely punctate, distinctly depressed along eye margin medially, narrow above but considerably wider below. Scape short, approximately 2× longer than width, first flagellar segment short, length 0.9 × apical width, middle flagellar segments 1.5–1.6 × as long as wide. ***Thorax***: Prothoracic spines rudimentary, little more than carinate angle. Mesoscutum shining, strongly punctate with punctures separated by 1–2 pw anteriorly and laterally, discal punctures widely separated; punctures of scutellum similar, dense laterally and posteriorly but very sparse, nearly impunctate anteriorly. Metanotum rugose. Mesepisternum, anterior to quadrately punctate mesepisternal groove, densely punctate; punctures slightly coarser than those of scutum, punctures less than 1 pw apart. Punctures of mesepisterna posterior to groove punctures similar to those of mesoscutum, dense anteriorly but sparser posteriorly and ventrally to 2–3 pw apart, interspaces shining. Hypoepimeral area shining with strong well-separated punctures; metepisternum shining, quadrately pitted. Metapleural prominence small, rugose, with short, curved carinate rim above small shining declivity. Propodeum with dorsal area shining, divided into irregular quadrate pits by longitudinal carinae, posterior surface of propodeal triangle shining, posterior propodeal surface outside triangle coarsely roughened, posterolateral mar-

gins of propodeum weakly carinate. Fore trochanter simple; fore femur slightly expanded mediodorsally, 3.6 × as long as broad; fore tibia 4.2 × as long as broad; hind tibia not expanded, 5.0 × as long as broad; posterior basitarsi 4.5 times as long as broad, sides parallel. ***Abdomen***: T1 shining: lateral and posterior punctures fine and dense but well separated on disc: sometimes with median impunctate line, apical margin depressed, apex narrowly translucent. T2–6 with surface shining, punctures fine and dense, roughly 1 pw apart, margins narrowly translucent. T7 strongly depressed, surface dull and densely punctate. Sterna weakly shining, with fine reticulate shagreening, fine punctures 1–2 pw apart throughout except on narrow, impunctate translucent margins; genitalia, S7 and S8 as illustrated (Figs. 3a–d); penis valves without dorsal wing; distal processes of S7 short and membranous. ***Vestiture***: Pile of face long, pale yellowish white, concealing facial surface except apex of clypeus exposed. Pile of vertex pale ochraceous, much sparser, fine hairs in ocello-ocular areas with denser, conspicuously branched hairs in and behind ocellar triangle. Pile of gena pale yellowish white near vertex, becoming whiter and longer below and on hypostomal area. Pile of mesoscutum and scutellum pale ochraceous. Pile of sides of thorax sparse, pale yellowish white with dense dorsolateral propodeal fringe pale ochraceous above. Hair of legs yellowish-white. T1 with long pale yellowish-white hair, dense laterally but very sparse medially, not extending to complete, white, apical fascia. T2–5 with complete, white, apical fascia, apical fascia absent on T6; T2–5 with hairs of disc very short, black, with increasing mix of longer, pale hairs posteriorly, lateral portions of T2–5 short, white. T6–7 with sparse, pale, appressed hairs. S1 with hairs white, sparse; S2–6 with pile white, that on discs simple, sparse and semi-appressed; apices S2–5 with distinct apical fascia of appressed, branched hairs, fascia strongest on S2 becoming progressively weaker on distal sterna. ***Color***: Black; antennae black to dark brown; mandibles with apical ⅔ translucent reddish brown; wings as in female; legs dark brown with tarsi ferruginous, tibial spurs pale brown.

Material examined.—Holotype ♀: USA: Texas: Bastrop Co: Sayersville (30° 12.99′ N, 97° 20.99′ W); 11-VI-1991; J. L. Neff; on flowers of *Sideroxylon lanuginosum* (deposited SEMC). Allotype ♂: same data as holotype (deposited SEMC). Paratypes: 18 ♂♂ and 2 ♀♀, same data as holotype: 1 ♂ and 1 ♀, same data except 9-VI-1986; 1 ♀, same data except 10-VI-1990 and taken in nest; 9 mm, same data except 3-VI-1992 and at flowers of *Sideroxylon lanuginosum*; 3 ♂♂, same data except 6-VI-1994; 2 ♂♂, same data except 17-VI-1994; 2 ♀♀, same data except 30-VI-1997; 1 ♀, Camp Swift Military Training Area, 12-VI-2003, A. Hook. Blanco Co.: 2 ♀♀, Pedernales Falls State Park (30°19.94′ N, 98°15.37′ W), 25-VI-1988, J. L. Neff, in nest; 2 ♂♂, same data except 2-VII-1988 and at flowers of *Sideroxylon lanuginosum*; 1 male same data except 27-VI-1997.

Etymology.—From the sapotaceous genus *Bumelia* Swartz, a junior synonym of *Sideroxylon* (Pennington 1990), the apparent sole pollen host of the species. I find *bumeliae* to be more mellifluous than names based on *Sideroxylon*. In addition, recent molecular studies suggest the resurrection of *Bumelia* for the American species of *Sideroxylon* may be justified as *Sideroxylon* appears to be paraphyletic (Anderberg and Swenson 2003).

Colletes incantipedis Neff, new species

Diagnosis.—The female of *Colletes incantipedis* is distinguished from all other American *Colletes* (except *C. bumeliae*) by the distinctive arrays of hooked setae on its foretarsi. Females can be distinguished from *C. bumeliae* by their smaller size, presence of dark hair on the vertex and mesoscutum, and more complete discal

punctation of T1. The males of *C. inuncatipedis* are very similar to males of *C. bumeliae* but are slightly smaller and differ in the shape of S7 and the well-formed propodeal spine (rudimentary in *C. bumeliae*).

Description.—♀. **Measurements**: (N = 10) BL: 6.6–7.8 mm; FW: 4.5–4.9 mm; HW 2.8–3.0 mm. ***Head***: Face 1.20–1.29 × wider than long, greatest distance between eyes exceeding eye length, inner orbits convergent below and arched inward above (UIOD 1.11–1.21 LIOD, UIOD 0.80 × 0.86 MIOD). Malar and clypeus as in *C. bumeliae* except clypeal striae irregularly convergent in medioapical impunctate area. Disc of supraclypeal area raised, shining, microstriate with strong, well-separated punctures; punctation of lateral surfaces smaller and much denser. Median line carinate from above supraclypeal area to preocellar triangle. Labrum, frons, vertex and facial fovea as in *C. bumeliae*. Gena as in *C. bumeliae* but slightly wider, width approx. 0.6 × eye width at level of antennal insertion. Flagellum as in *C. bumeliae*. ***Thorax***: Thorax and legs as in *C. bumeliae* except forebasitarsis slightly longer and narrower; basal width 0.33 × length; length 0.60 × length of foretibia. ***Abdomen***: Terga as in *C. bumeliae* except discal punctation stronger, more uniform, without median impunctate area. Punctation of sterna similar to *C. bumeliae* but coarser, particularly on S6 where apical punctures are strong and dense. ***Vestiture***: Pile of face as in *C. bumeliae* except vertex with mixture of yellowish-white and darker brown to black hair. Pile thorax as in *C. bumeliae* except brown to black hair sparsely mixed among pale pile of scutum. Hair of legs *C. bumeliae*. Pile of terga as in *C. bumeliae* except T-5 without pale apical fascia. Pile of sterna darker and denser, particularly on distal ½ of S6. ***Color***: Black, except apical half of mandibles, tibial spurs, and tarsal claws dark reddish brown; apices of T 1–4 and S 1–5 narrowly translucent brown. Tegulae dark brown to black; wings hyaline, with abundant short dark hairs, veins dark brown with pterostigma dark brown.

♂.—**Measurements**: (N = 7), BL: 6.3–7.4 mm; forewing 4.3–5.3 mm, HW 2.6–2.9 mm. ***Head***: Face 1.20–1.24 × wider than long, greatest distance between eyes slightly greater than eye width; inner margins strongly convergent below and weakly incurved above, UIOD distance 1.31–1.41 × LIOD, UIOD 0.91–0.94 × MIOD. Malar space 0.4 times as long as wide. Clypeus densely, finely, punctate, discal punctures slightly sparser apically, apical margin narrowly depressed. Labrum with disc evenly rounded, impunctate and shining. Supraclypeal area densely punctate, medial punctures roughly twice diameter of peripheral punctures. Median line carinate from apex of supraclypeal area to just below median ocellus. Punctures of frons coarse and dense. Facial fovea well defined, narrow, expanded subapically, upper portions of facial fovea strongly depressed along edge of eyes, outer margins carinate, surface of fovea dull. Punctures of vertex fine, dense with impunctate space laterad of ocelli. Gena shining, finely punctate, distinctly depressed along eye margin medially, narrow above but considerably wider below. Scape strongly punctate, short, approximately 2× longer than apical width; first flagellar segment short, length 0.9 × apical width; middle flagellar segments 1.5–1.6 × as long as wide. ***Thorax***: Prothoracic spines short and sharp. Mesoscutum shining, strongly punctate with punctures separated by 1–2 pw anteriorly and laterally, discal punctures 2–3 pw apart; punctures of scutellum similar, dense laterally and posteriorly but very sparse, nearly impunctate anteriorly. Mesepisterum, anterior to quadrately punctate mesepisternal groove, densely punctate, punctures slightly coarser than those of scutum, punctures less than 1 pw apart. Punctures of mesepisterna posterior to groove similar to those of scutum, dense anteriorly but sparser posteriorly and ventrally to

2–3 pw apart, interspaces shining. Hypoepimeral area shining with strong well separated punctures. Metepisternum shining, quadrately pitted; metapleural prominence small, rugose, with short, curved carinate rim above small shining declivity. Propodeum as in *C. bumeliae*. Foretrochanter simple; forefemur slightly expanded mediodorsally, 3.6 × as long as broad; fore tibia 4.2 × as long as broad; hind tibia not expanded, 5.0 × as long as broad; posterior basitarsi 4 × as long as broad, sides parallel. ***Abdomen***: T1 shining, lateral and posterior punctures fine and dense but well separated on disc, apical margin depressed and narrowly translucent. T2–6 with surface shining, punctures fine and dense, roughly 1 pw apart, margins narrowly translucent. T7 strongly depressed, surface dull and densely punctate. Sterna weakly shining, with fine reticulate shagreening, fine punctures 1–2 pw apart throughout except on narrow, impunctate translucent margins; genitalia and S8 as in *C. bumeliae* (Figs. 3a–d), S7 as figured (Fig. 3e) with elongate, strong distal processes (not short and membranous as in *C. bumeliae*). ***Vestiture***: as in *C. bumeliae*. ***Color***: Black; antennae black to dark brown; mandibles with apical ⅔ translucent reddish brown; wings as in female; legs dark brown with tarsi ferruginous, tibial spurs pale brown.

Material examined.—Holotype ♀. USA: Texas: Bastrop Co., Bastrop, 0. 5 mi. N (30° 08.11′ N, 97° 19.24′ W), J.L. Neff, 30-VI-1997. on flowers of *Sideroxylon lanuginosum* (deposited SEMC). ♂: same data as holotype (deposited SEMC). Paratypes: 3 ♀♀ and 19 ♂♂, same data as holotype. 13 ♀♀, same data as holotype except 17-VI-1998. Travis Co.: 1 ♂, Austin, BFL (30° 17.10′ N, 97° 46.83′ W), 6-VI-1986, J. L. Neff, on flowers of *Eysenhardtia texana*; 1 ♂, same data except 12-VI-1987 and on flowers of *Sideroxylon lanuginosum*; 2 ♂♂, same data except 18-VI-1987; 1 ♂, same data except 24-VI-1997.

Etymology.—The name refers to the unusual arrangement of hooked setae on the foretarsi and is a combination of *inuncantis* (Latin—covered with hooks) and *pedis* (Latin—leg).

BIOLOGY

We have occasionally encountered males of *Colletes bumeliae* nectaring at, and patrolling, the flowers of *Eysenhardtia texana* Scheele (Fabaceae) and one male bore pollinia of Asclepiadaceae on its mouthparts, but males of *C. bumeliae* and *C. inuncantipedis* are normally observed only about flowers of *Sideroxylon lanuginosum* (A. Michaux) Pennington (Sapotaceae) (= *Bumelia lanuginosa*) (Fig. 1b). Females of *C. bumeliae* and *C. inuncantipedis* have only been observed at flowers of *S. lanuginosum*, with most females bearing scopal loads or extensive loads of pollen on their foretarsi. All scopal pollen loads examined consisted solely of *Sideroxylon* pollen (n = 20). All evidence points to both species being oligolectic on *Sideroxylon*.

Sideroxylon lanuginosum is a widespread tree or shrub (2–15 m tall) of the Southeast and South Central U.S.A. and adjacent Mexico, commonly known as gum bumelia, gum elastic, chittamwood or woolybucket bumelia (Cheatham et al. 2000). *Sideroxylon lanuginosum* normally flowers in middle to late June in central Texas, producing large numbers of small, pale, short-lived, nectiferous flowers. The tubular, distally spreading corolla is 3–4 mm long. Each flower has five fertile anthers, each of which is subtended by a petaloid staminode. The anthers are not included in the basal floral tube but rather are partially hidden in the distal folds of the corolla (Fig. 1b). I have observed female *C. inuncantipedis* first inserting their heads into the corolla, apparently to lap nectar, and then inserting their forelegs into the corolla, apparently to gather pollen (Fig. 1a). The hooked foretarsal hairs of female *C. bumeliae* and *C. inuncantipedis* often bear much *Sideroxylon* pollen and obviously aid in extracting pollen from the partially hid-

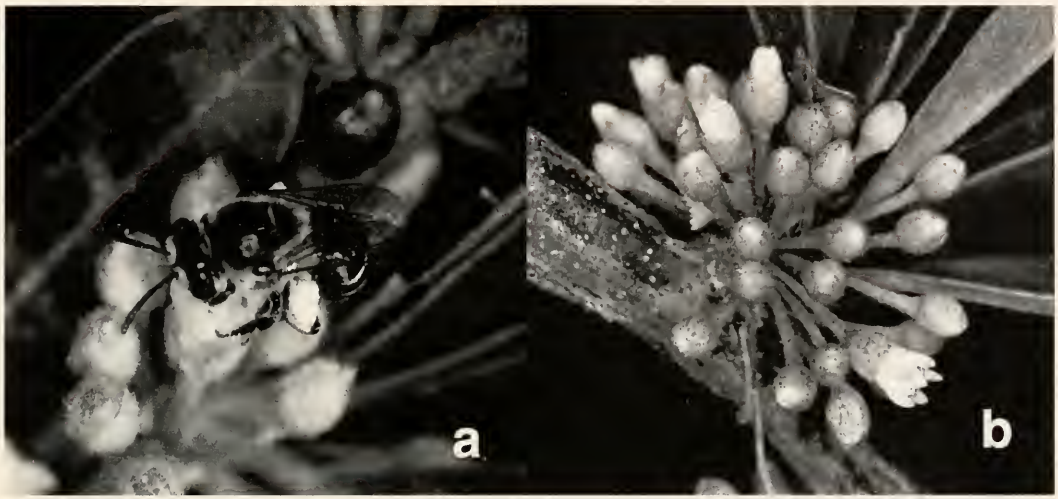

Fig. 1. Flowers of *Sideroxylon lanuginosum*. a. Pollen-collecting female of *Colletes inuncantipedis* inserting forelegs into corolla. b. *Sideroxylon* inflorescence.

den anthers. The exact mechanics of how *C. bumeliae* and *C. inuncantipedis* extract pollen of *S. lanuginosum* has yet to be determined because most pollen collecting visits are relatively rapid (< 5 sec), and occur high in the canopy. The foretarsi, with their arrays of hooked hairs, apparently are pulled over the anthers which are partly hidden by the lateral folds of the corolla and the subtending staminodes. This pollen collecting behavior appears to be analogous to that of various *Calliopsis* (*Verbenapis*) spp. which employ hooked tarsal hairs to extract pollen from anthers hidden in the narrow corollas of various Verbenaceae (Shinn 1967), with the obvious difference that the corollas of *Sideroxylon* are not particularly narrow and the anthers are much more exposed.

While the adjusted combined length of the femur and tibia of the forelegs does not differ between *C. bumeliae* and *C. inuncantipedis* and a sample of North American *Colletes* (0.871 ± .032 (n = 19) vs. 0.881 ± .044 (n = 75), p = .3408, unpaired t-test), the adjusted foretarsal lengths of *C. bumeliae* and *C. inuncantipedis* are significantly shorter than average of the sample of North American *Colletes*, (0.490 ± .011, (n = 18) vs. 0.511 ± .034, n = 75, P < .0001, unpaired t-test).

The foretarsal arrays of hooked setae of females of *Colletes bumeliae* and *C. inuncantipedis* are apparently unique among Nearctic and Neotropical *Colletes* species (Figs. 2a, b). The foretarsi of most New World *Colletes* I have examined only bear simple hairs (Figs. 2e, f), although the females of few species, such as *C. skinneri* or *C. wootoni*, have foretarsal combs with dense arrays of apically hooked hairs (Figs. 2c, d). The function of the hooked hairs for these bees is unclear as neither is closely associated with tubular flowers. *Colletes wootoni* apparently is polylectic while *C. skinneri* appears to be oligolectic on papilionoid legumes (J. L. N. pers. obs.).

The foretarsal combs of *C. bumeliae* and *C. inuncantipedis* are remarkably similar to the those found on the foretarsi of the females of the west Palearctic species, *C. nasutus* Smith. *Colletes nasutus* is oligolectic on *Anchusa* (Boraginaceae) and uses its foretarsal arrays to extract pollen from the anthers included in the narrow corolla tubes (Müller 1995). Females of *C. nasutus* differ from *C. bumeliae* and *C. inuncanti-*

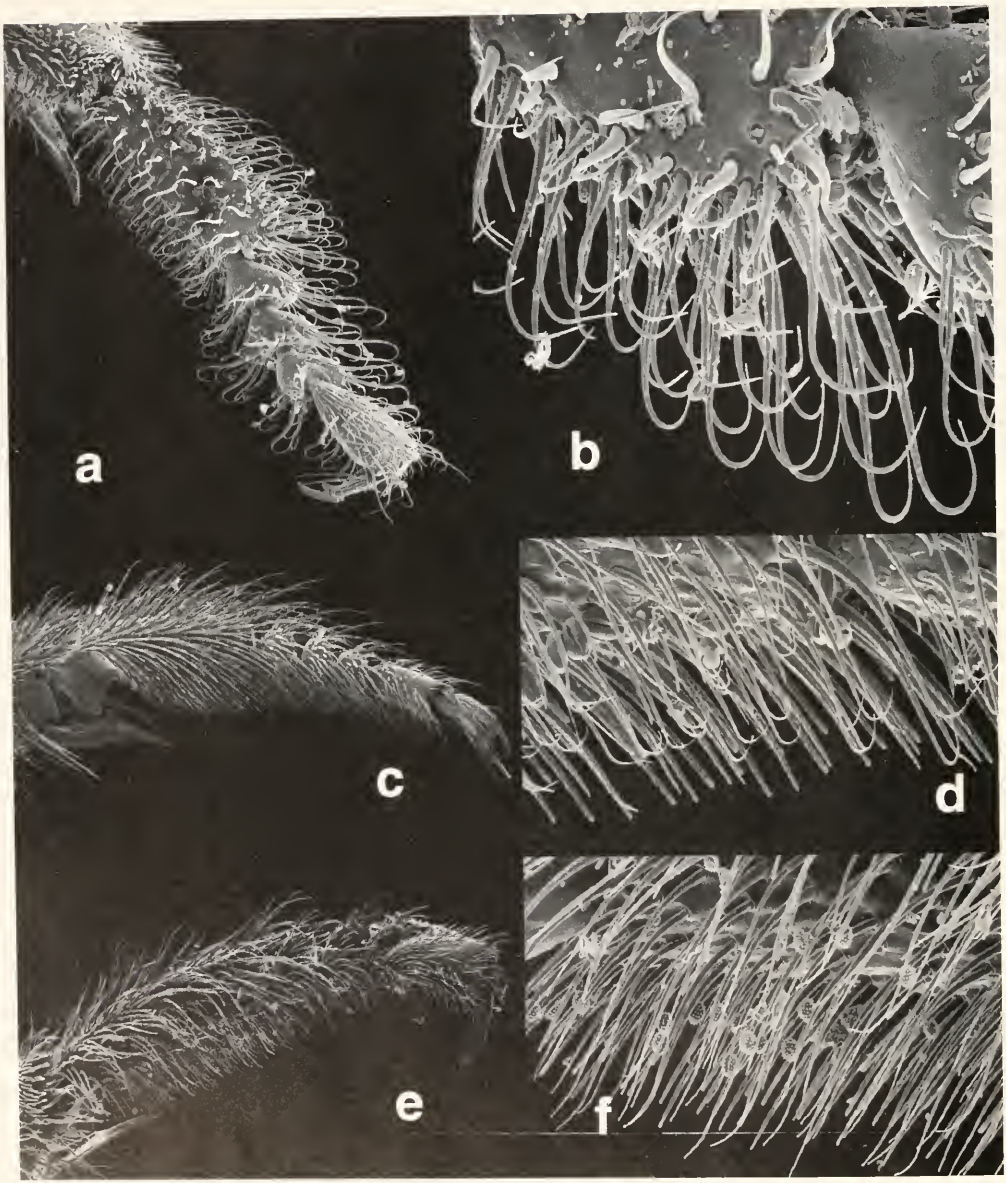

Fig. 2. Foretarsi of female *Colletes* with closeup of foretarsal setae. a, b. *Colletes inuncantipedis*. c, d. *Colletes wootoni*. e, f. *Colletes birkmanni*.

pedis in having foretarsi of normal length but elongate forefemora and -tibiae, apparently an adaptation for extracting pollen hidden in narrow corolla tubes (Müller 1995). Shortened foretarsi (and modified forefemora) are found in two closely related European *Colletes* whose foretarsi bare arrays of stout, flattened, curved setae. These two species, *C. anchusae* Noskiewiscz and *C. wolfi* Kuhlmann, are oligolectic on *Cynoglottis* (Boraginaceae) and use their tarsal setal arrays to extract pollen from the narrow floral tubes of *Cynoglottis* flowers (Müller and Kuhlmann 2003).

Müller (1995) and Müller and Kuhl-

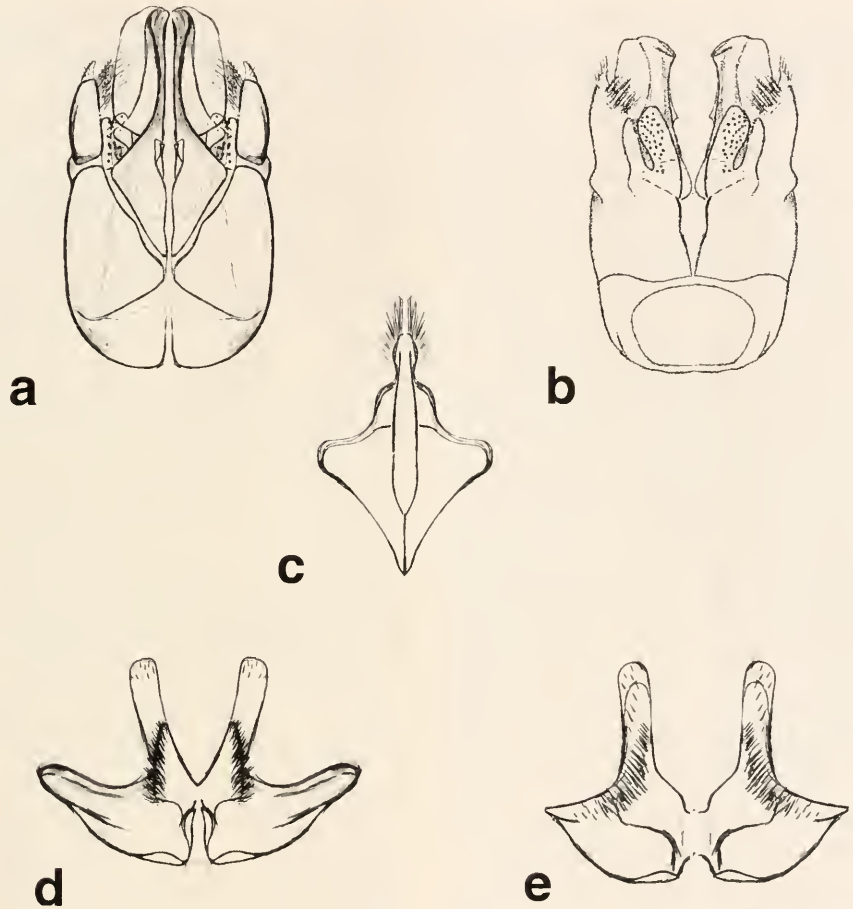

Fig. 3. Genitalia and associated sterna. a. dorsal view, genital capsule, *Colletes bumeliae*. b. ventral view, genital capsule, *C. bumeliae*. c. S8, dorsal view, *C. bumeliae*. d. S7, dorsal view, *C. bumeliae* e. S7, dorsal view, *C. inuncantipedis*.

mann (2003) used forewing length as their measure of body size, rather than headwidth. Curiously, when either internal or total wing length was used in the denominator when adjusting for body size in the comparison of American bees, no significant difference was found between the tarsal lengths of females with and without hooked hairs (0.306 ± 0.007 (n = 19) vs. 0.302 ± 0.027 (n = 75), p = 0.5488 or 0.255 ± 0.008 (n = 18) vs 0.254 ± 0.022, (n = 65), P = 0.8390). However, there are several reasons why wing length may be a less than ideal estimator of body size in many bee groups. First, wing length is often compromised by wing wear. Second, wing length is expected to be an accelerating, positive function of body size due to considerations of wing loading (Danforth 1989). In addition, the use of internal markers of wing venation to avoid problems of wing wear in estimating wing length may further complicate matters since wing venation extends distally with increasing body size (Danforth 1989). Head width was more strongly correlated with transtegular distance (another measure of body size), than was wing length (R = .945 vs. R = .894) in the sample of American *Colletes*, suggesting it should be a superior estimator of body size, at least among groups like *Colletes* which lack ob-

vious cephalic allometry. Ultimately, these estimators will need to be tested against actual body dry weight.

Nests of *C. inuncantipedis* are unknown but nests of *C. bumeliae* were discovered in deep sandy soils near Sayersville, Bastrop Co., Texas, as well as in sandy alluvial deposits along the Pedernales River at Pedernales Falls State Park, Blanco Co., Texas. Nests near Sayersville were loosely grouped along a heavily shaded, unpaved road through a post oak woodland. At Pedernales Falls, nests were scattered along a road cut through the alluvial deposits with one group of 5–7 nests clustered within the entrance of a large, abandoned mammal (armadillo?) burrow. Two nests were excavated, one each at Pedernales Falls and one at Sayersville, both with similar structure. The excavated nest at Sayersville, and other nearby nests, were on level ground and had a simple fan like tumulus formed of soil pushed away from the entrance. Entrances to the nests at Pedernales Falls were in a near vertical bank and thus lacked tumuli. The first 15–20 cm of the main burrows descended gradually to a depth of 5–10 cm before descending almost vertically. Both nests were lost before reaching any cells, the Sayersville nest at 40 cm and the Pedernales Falls nest at 28 cm. In both cases, the problem was backfilled laterals. Burrows were unlined and had an interior diameter of 5.0–5.5 mm. In both cases, the burrows each had several soil septa, each 5–10 mm thick. No cells were recovered at Sayersville but eight single cells were recovered from the Pedernales Falls excavation at depths of 30–50 cm. All cells were horizontally oriented and from 10 to 15 cm from the estimated location of the main burrow. Individual cells were of the classic membranous sandwich bag type with a folding closure (Torchio et al. 1988). One cell recovered intact was 11 mm long with a maximal diameter of 7 mm. Each cell had a collar, roughly 5 mm in diameter, which extended 3 mm from the cell entrance. Pollen in the semi-liquid provisions was 100% *Sideroxylon*.

Most pollen foraging occurs between 0900 and 1400 CDST, with some foraging as late as 1630 hrs. Full daily provisioning series for three females indicated they made 11–12 pollen trips per day. Mean pollen trip duration was 19.3 ± 6.7 min (n = 73, 9–38). Time in the nest between pollen trips averaged 4.9 ± 2.5 min (n = 72, 2–21).

Since *C. bumeliae* and *C. inuncantipedis* are often locally abundant and contact with the anthers and stigma of *S. lanuginosum* by both males and females is unavoidable during foraging, these bees potentially are important pollinators of *S. lanuginosum*. However, as they are small bees visiting a large tree, actual pollinator efficacy needs to be demonstrated directly, or at least inferred from degree of pollen carryover and frequency of interplant moves in order to have any confidence in statements on its importance as a pollinator. The overall importance of these bees in the reproductive biology of *S. lanuginosum* is probably not great since they appear to be much more restricted in distribution than the tree. Even in central Texas, the most common visitors of gum bumelia are often various wasps, particularly the fast flying males of *Myzinum* spp. (Tiphiidae), as well as males of various halictid and megachilid bee species, rather than *C. bumeliae* or *C. inuncantipedis*.

Colletes bumeliae and *C. inuncantipedis* are currently known from only five sites in three counties in central Texas. Although their ranges overlap, they have not been found together at the same site. In all cases, the sites had both *S. lanuginosum* and some nearby areas of sandy soils. The ranges of these two species are likely to expand with further collecting since the fauna of *Sideroxylon* flowers is very poorly known. Despite the wide distribution of the genus, there are no records of any hymenopterous visitors to either *Sideroxylon*

or *Bumelia* in the *Hymenoptera Catalog* (Krombein et al. 1979).

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A New Afrotropical Species of the Wasp Genus *Dolichurus* (Hymenoptera: Apoidea, Ampulicidae)

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Abstract.—The new species ***Dolichurus foroforo***, widely distributed from west to east Africa, is described. It is compared with all currently recognized Afrotropical species of the genus. The new species is mainly characterized by its unusual coloration: in the female, the scape, apical margin of frontal platform, clypeus, tibiae, and tarsi are orange. In the male, the apical margin of frontal platform, pronotal tubercles, and tegulae are white, whereas most of the antennae and legs are bright orange. Additionally, metasomal terga I–III are coarsely, densely punctate (only laterally so in the female).

Dolichurus is a cosmopolitan genus of mostly black, rather small cockroach-hunting wasps. The genus belongs in the Ampulicidae, which is basal within Apoidea (bees and the paraphyletic Sphecidae). It is considered to represent the sister group to all about 30,000 species of Apoidea, or to be one of its basalmost lineages (Melo 1999). *Dolichurus* has 49 species distributed by regions as follows (including the species described herein): Nearctic 1, Neotropical 2, Palearctic 5, Ethiopian 10, Oriental 27, and Australian 4. Australia and parts of the species-rich Oriental fauna were revised recently (Krombein 1979 for Sri Lanka, Tsuneki et al. 1992 for the Philippines, Tsuneki 1992 for southeast Asia, Ohl 2002 for Australia), but most parts of the world are still in need of taxonomic treatment.

Nine species and one subspecies of *Dolichurus* in sub-Saharan Africa are currently recognized (the current known distribution is given in parentheses, with the country of the type locality marked by an asterisk*):

Dolichurus basuto Arnold, 1952 (Lesotho*)
Dolichurus bimaculatus Arnold, 1928 (Democratic Republic of Congo, Zimbabwe*)
Dolichurus guillarmodi Arnold, 1952 (Lesotho*)
Dolichurus ignitus F. Smith, 1869 (Central African Republic, Democratic Republic of Congo, Rwanda, South Africa*, Tanzania)
Dolichurus ignitus contractus Arnold, 1951 (Ethiopia*)
Dolichurus kohli Arnold, 1928 (South Africa*)
Dolichurus quadridentatus Arnold, 1940 (Democratic Republic of Congo*)
Dolichurus rubripyx Arnold, 1928 (South Africa*)
Dolichurus secundus de Saussure, 1892 (Madagascar*) (= D. *tertius* de Saussure, 1892)
Dolichurus venator Arnold, 1928 (Zimbabwe*)

Kohl (1893) was the first to treat the Ampulicidae on a comprehensive and worldwide basis, but he only listed the eleven species of *Dolichurus* known to him and copied or summarized their descriptions. He mentioned the three species from Africa described by Smith (1869) and Saussure (1892). In his revision of African *Dolichurus*, Arnold (1928) reported five species, and he described some others in subsequent publications (Arnold 1940, 1951, 1952). No African *Dolichurus* has been described in the last decades, and most already described species are known from very few specimens or even the types only.

Most Ampulicidae typically run over the ground or on tree trunks and are frequently overlooked by collectors. As a consequence, *Dolichurus* has also been essentially rare in collections until recently, when improved collecting methods (particularly Malaise traps) have revealed a remarkable amount of material even from remote areas of the world. Thus, the comparatively low number of currently recognized species from Africa south of the Sahara is a collecting artifact rather than an appropriate representation of the true species number in this diverse area. We recently started to revise African *Dolichurus*, and the material from a few collections only apparently represents 15 or more undescribed species. One of these species is morphologically quite distinctive and is represented by several specimens in both sexes from west to east Africa. It is herewith described as a first step towards a comprehensive revision of the genus in the Afrotropical region.

Methods and Abbreviations

Measurements, Terminology, and Abbreviations.—Measurements and ratios were taken following the standards proposed by Ohl (2002). Measurements were made using an ocular micrometer on a LEICA MZ12 microscope and are in millimetres. **Body length** in females is measured from the apex of the pronotal platform to the apex of the tube formed by metasomal sternum VI, and in males from the apex of the pronotal platform to the posterior margin of tergum III (subsequent terga may be artificially exposed to varying degrees). The **forewing length** is taken from the apex of the humeral plate at wing base to the extreme wing tip. The **flagellomere-I-ratio** is the maximum length of flagellomere I divided by its apical width (in dorsal view). The **eye ratio** is the shortest lower interocular distance across clypeus divided by shortest upper interocular distance across ocellar area. The **oculo-ocellar-ratio** is the shortest distance between a lateral ocellus and the eye margin divided by a midocellar diameter.

Terminology for general morphology follows Bohart and Menke (1976), with a few additions for *Dolichurus* by Ohl (2002). Distinction is made between the true abdomen (with the propodeum as its first segment) and the **metasoma** (excluding it). Accordingly, the propodeum is included as part of the mesosoma, but is excluded from the thorax. The **frontal platform** (lamella of Tsuneki 1992) is a median, U-shaped and platform-like extension of the frons overhanging the antennal bases. The **pronotal tubercles** are more or less prominent, dorsolateral swellings of the pronotal collar, which are separated by a median sulcus. The **metapostnotum** is usually referred to as 'propodeal triangle', 'triangular area' or 'propodeal enclosure' in Apoidea, but is in fact the metathoracic postnotum that is fused to the true propodeum (Brothers 1976). We follow Melo (1999) in differentiating **omaular carina** and **omaular sulcus.** The **episcrobal area** (= hypoepimeral area of Bohart and Menke 1976) is the upper portion of the mesopleuron posterodorsally of the episternal sulcus and the scrobal sulcus.

Scanning Electron Microscopy.—Specimens were examined using a LEO 1450VP scanning electron microscope. They were first removed from the pins and were then mechanically cleaned by removing obvious dirt and other debris. Finally, they were sputter-coated with gold-palladium.

Sources of Material.—Abbreviations used to indicate depositories of specimens are listed below with corresponding institutions and personal collections. When appropriate, the name persons who arranged the loans of material are mentioned in parentheses.

CAS California Academy of Sciences, San Francisco, USA (W. J. Pulawski).

OHL Personal collection of M. Ohl, Berlin, Germany.

UCD Bohart Museum of Entomology, University of California, Davis, USA (S. Heydon, R. M. Bohart).

Dolichurus foroforo n. sp.
(Figs 1–8)

Derivation of name.—The new species is named after the collecting locality of the holotype and most paratypes, Foro Foro in the Ivory Coast. It is a noun in apposition.

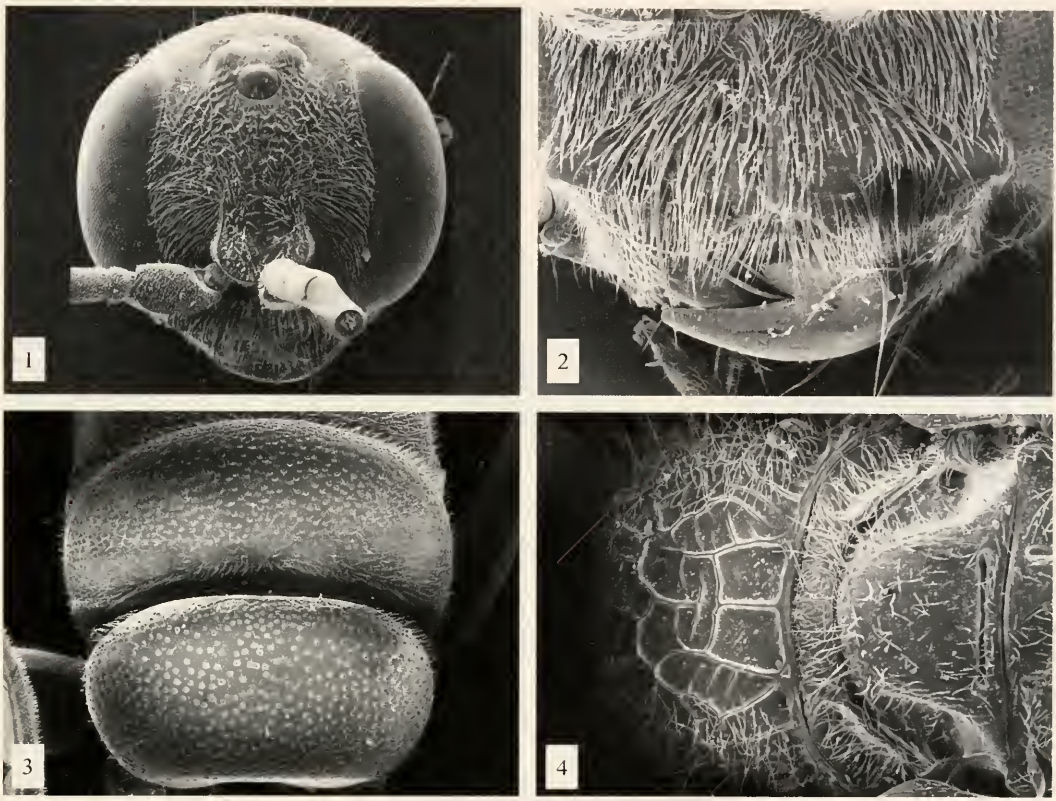
Diagnosis.—In the absence of a comprehensive revision of Afrotropical *Dolichurus*, comparison of *D. foroforo* with other species of the genus is difficult. Additionally, most currently recognized African *Dolichurus* are known from one sex only. We have studied approximately 20 African species of *Dolichurus*, most of which are undescribed, and the revision by Arnold (1928) and the original descriptions of all African species and subspecies. In most cases, Arnold's descriptions provide sufficient details for a reliable differentiation of *D. foroforo* from already described species. We conclude that the new species differs from all currently recognized African species of the genus in a unique combination of characters.

Females of *D. foroforo* are unique among African *Dolichurus* in the combination of the following characters: lateral portions of metasomal terga I–III with coarse, dense punctation (Fig. 7; metasomal punctation indistinct in most *Dolichurus*); scape, apical margin of frontal platform, and clypeal apex orange (black in most species); and coxae and femora brown, contrasting with orange tibiae and tarsi (legs uniformly colored in most African *Dolichurus*). Females of *D. foroforo* are similar to most African *Dolichurus* in having some apical metasomal segments red or orange (completely black or dark brown in *D. secundus*, *D. kohli*, *D. guillarmodi*, and one undescribed species). Among the species with a bicolored metasoma, *D. basuto* and *D. venator* have tergum III and the basal margin of tergum IV black (tergum III apically red in *D. foroforo*, besides other structural differences). Terga I–III are impunctate or have a very few minute, widely scattered punctures in *D. quadridentatus*, *D. ignitus*, and *D. rubripyx* (coarsely, densely punctate in *D. foroforo*; Fig. 7).

Males of *D. foroforo* are unique among African *Dolichurus* in the remarkable body coloration: the apical margin of the frontal platform, the pronotal tubercles, and the tegula are clearly marked with white, and most of the antennae and legs are bright orange. Additionally, male *D. foroforo* have the metasomal terga I–III coarsely, densely punctate (punctures no more than one diameter apart; Fig. 3). *Dolichurus bimaculatus* and *D. basuto* are similar in having largely orange legs, but *D. bimaculatus* has two white clypeal markings (clypeus black in *D. foroforo*), lacks white markings on the pronotal tubercles (present in *D. foroforo*), and has a markedly coarse, areolate face sculpture, which extends to the hindocelli (face sculpture not markedly coarse, irregular, not extending beyond midocellus in *D. foroforo*; Fig. 1). *Dolichurus basuto* also has white pronotal tubercles but the frontal platform and the tegula without white. The tergal punctation is also sparser in *D. bimaculatus* and *D. basuto* than in *D. foroforo*: at least some punctures along tergal midline are about three diameters apart and rather irregular in the former species, whereas one diameter apart and appearing markedly dense and regular in *D. foroforo* (Fig. 3).

Description.—Black. The following are orange: mandibles (tip narrowly black), antennae (slightly darker dorsally), and legs (except for tarsomere V, most of femora, and coxae). Wings hyaline to indistinctly infumate.

Face (Figs. 1–2) below antennae with dense, appressed, silvery setae; head otherwise and mesosoma with numerous erect, whitish setae, on mesosoma shorter ventrally. Metasoma with short, indistinct, white setae, each arising from a distinctive puncture (Fig. 3). Vestiture generally sparser in females than in males; female



Figs. 1–4. *Dolichurus foroforo,* male. 1, head in frontal view. 2, clypeus and mandibles. 3, terga I–II. 4, scutellum, metanotum, and metapostnotum.

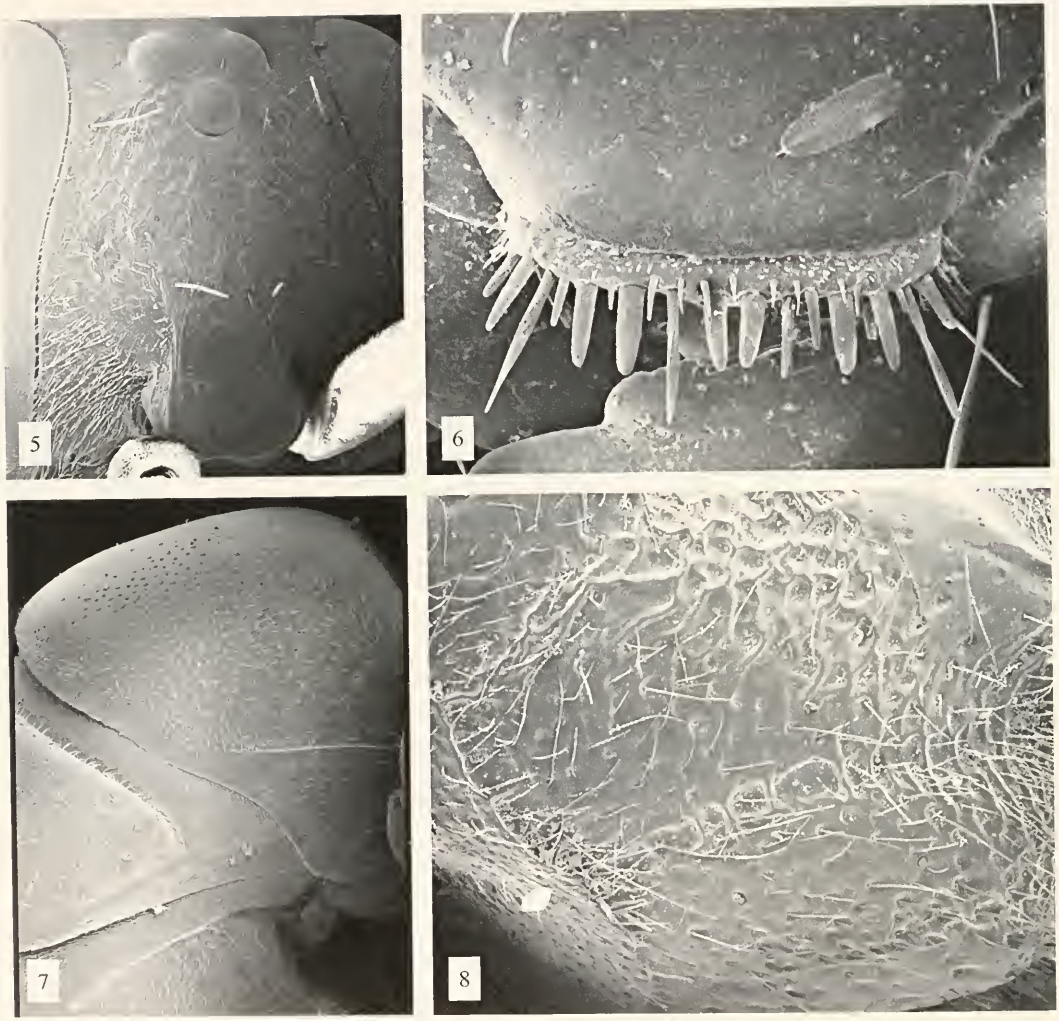
metasoma predominantly without setation.

Face with rugulae laterally of midocellus oblique (Fig. 1). Vertex markedly shiny, with numerous scattered, shallow punctures.

Pronotal dorsum transversely rugose between tubercles, with distinct transverse carina; sides almost completely smooth and shiny. Mesopleuron obliquely rugose toward posterior margin. Omaular sulcus (as in Fig. 8) present, coarsely pitted, markedly bent posteriorly and fused with anterior section of scrobal sulcus before meeting tegula. Omaular carina sharp, ventrally continued by sharp, somewhat elevated acetabular carina. Midline of acetabular area posteriorly terminating in small, blunt tooth between markedly convex portions of acetabular carina. Sternaulus present, coarsely sculptured (Fig. 8). Coarsely pitted remnant of episternal sulcus meeting end of omaular carina at obtuse angle. Metanotum longitudinally rugose (Fig. 4). Metapleuron shiny, with a few irregular longitudinal rugulae dorsally. Metapostnotum with five to seven irregular longitudinal and a varying number of transverse carinae (Fig. 4); posteriorly delimited by lamellate carina. Propodeal hindface irregularly, coarsely rugose; laterally delimited by irregular carina, with small tooth-like projection at lower end.

Female: Metasomal segments IV–VI and apical margin of III orange.

Mandible tridentate. Clypeal lobe markedly protruding, somewhat overhanging mandibles, apically truncate, shiny (Fig. 6); median carina confined to basal half of



Figs. 5–8. *Dolichurus foroforo*, female. 5, frons in oblique frontal view. 6, clypeus. 7, lateral portion of tergum I. 8, mesopleuron.

clypeus. Margin of frontal platform markedly bulging (Fig. 5). Flagellomere I 1.1× as long as II, length of flagellomeres II–IV subequal, following flagellomeres becoming progressively shorter. Frons between base of frontal platform and midocellus densely, rather finely rugose; rugulae laterally of midocellus oblique (Fig. 5).

Punctation of scutum and scutellum markedly sparser medially than laterally. Mesopleuron punctatorugose throughout (Fig. 8). Longitudinal rugulae on propodeal sides markedly developed.

Terga I–III and sterna II–III densely punctate laterally (Fig. 7), punctures widely scattered medially. Metasomal segments IV–VI virtually impunctate.

Body length 7.5–10.6 mm; forewing length 4.1–5.3 mm; flagellomere-I-ratio 4.6–5.0; eye ratio 1.2–1.3; oculo-ocellar-ratio 1.3–1.5.

Male: Apical margin of frontal platform orange (partly infused by white). Pronotal tubercle, anterior margin of frontal platform, and tegula with white markings.

Mandible broad, robust, bidentate (Fig.

2). Clypeus (Fig. 2) coarsely punctatorugose; with median carina, terminating in small, blunt tubercle; median clypeal lobe broadly deeply emarginate, emargination flanked by obtuse tooth. Frontal platform about as broad as long; indistinctly punctate in distal two-thirds; margin indistinctly bulging. Scape with ventral carina. Length of flagellomeres I–III subequal, following flagellomeres becoming progressively shorter. Frons between base of frontal platform and midocellus densely, coarsely rugose (Fig. 1).

Scutum, scutellum, and metanotum shiny, almost uniformly, shallowly punctate, punctures at least one diameter apart (Fig. 4). Propodeal side with rather regular, coarse, oblique rugulae; smooth anteriorly.

Terga coarsely, densely punctate throughout (Fig. 3); slightly sparser along midline of terga I–II; punctation very dense on tergum III, most punctures not more than 1.0 diameters apart. Sterna coarsely punctatorugose throughout. Sternum II markedly bulging anteriorly; with weakly developed basal, transverse carina and sulcus. Sternum III with sharply delimited, markedly depressed posterior margin.

Body length 5.6–6.9 mm; forewing length 3.4–4.6 mm; flagellomere-I-ratio 3.5–4.0; eye ratio 1.1–1.0; oculo-ocellar-ratio 1.1.

Life History.—Nothing is known about the life history of *D. foroforo*. A few males (from Togo, Kenya, and probably that from Senegel) have been collected by hand net, and the male from Ethiopia in a Malaise trap. There is no explicit information on the collecting method of the numerous specimens from Foro Foro (Ivory Coast), but it is likely anyway that they have been collected by yellow pan traps as part of an experimental agricultural survey as documented by Duviard (1973). Duviard set out yellow pan traps in selected heights above ground (0 cm, 50 cm, 100 cm, 150 cm, 200 cm) in different habitats. The label data imply that the *Dolichurus* from Foro Foro have also been collected as part of this survey: D. Duviard is the collector, "Foro Foro/Bouaké/Ivory Coast" is the type locality, a period of a few days is given as collecting time, and finally, a smaller, second label gives 0 cm, 50 cm, 100 cm, and 200 cm.

The collecting locality is the "Forêt Classée du Foro Foro" (07°55'00"N 004°59'00"W), and details on the climate and the vegetation of the type locality of *D. foroforo* are given in Duviard (1973). Six males and fourteen females of *D. foroforo* have been collected in this area. Five of the males were trapped on ground level (0 cm) and one male at 50 cm. Labels with height information are absent in three females, and the remainder were collected as follows: 0 cm four females, 50 cm three females, 100 cm three females, and 200 cm one female. These results imply that males used to fly in low height above ground, whereas females seem to occur regularly from ground level to 150 cm. This probably reflects that searching strategies of females are different from males, because females primarily search for prey and for potential nesting sites, whereas males search for females. However, the number of specimens with data on flight height is too limited for significance tests.

Type material.—**Holotype:** male, IVORY COAST: Foro-foro, Bouaké, Afr[ique], D. Duviard, 17–19 Jan 1971 (CAS).

Paratypes (10 ♂, 14 ♀). same data as holotype, but, 23–25 Aug 1971, 13–15 Sep 1971, 27–28 Sep 1971, 27–29 Sep 1971, 29 Nov–1 Dez 1971 (3 ♂, UCD), 14–16 Dec 1970, 28–30 Dec 1970, 6–8 Jan 1971, 17–19 Jan 1971, 05–07 July 1971, 30 Aug–01 Sep 1971, 50cm, 15–17 Nov 1971, 29 Nov–01 Dec 1971, 13–15 Dec 1971, 21 Jan–03 Feb 1973, 1972 [no specific date], 1974 [no specific date] (10 ♀, UCD). [1 ♀ and 1 ♂ each in the Museum für Naturkunde, Berlin, The Natural History Museum, London, and the California Academy of Sciences, San Francisco.]

SENEGAL: Koumpentoum, Dec 1975, G. Couturier (1 ♂, UCD).

TOGO: Amaoudé, 17 km N Sokodé, 18 Feb 1991, W. J. Pulawski (2 ♂, CAS).

ETHIOPIA: Langano, ~1600m, 7°35'N 38°42'E, 8–12 Apr 1958, Malaise Trap [collector unknown] [1 ♂, OHL].

KENYA: Rift Valley Province, Marich Pass Field Studies Centre, 1°32.2'N 35°27.4'E, 9 Jun 1999, W. J. Pulawski and J. S. Schweikert (1 ♂, CAS).

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A Review of the Genera of Oligositini (Hymenoptera: Trichogrammatidae) with a Preliminary Hypothesis of Phylogenetic Relationships

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Abstract.—The twelve genera of the tribe Oligositini (Trichogrammatidae: Oligositinae) are reviewed. The genus *Brachistagrapha* De Santis is removed from the tribe and synonymized with *Chaetogramma* Doutt, a member of the Trichogrammatini (**new synonymy**). Phylogenetic analysis supports the recognition of two subtribes, the Oligositina and Eteroligositina. The large cosmopolitan genus *Oligosita* Walker is found to be polyphyletic and its current species are assignable to both subtribes. Those transferred to the Eteroligositina are now placed in the resurrected genus ***Pseudoligosita* Girault,** long considered a synonym of *Oligosita*. However, the removal of these species does not render *Oligosita* monophyletic. Remaining problems in the classification of the Oligositini are discussed. Included are a brief synopsis of each genus and a key to genera.

This study was prompted by an attempt to define *Oligosita* Walker, the most speciose genus of Trichogrammatidae. An examination of species soon suggested that two or more independent lineages existed within this common and cosmopolitan genus. Furthermore, it appeared that the tribe Oligositini could be divided into two broad phenetic groups of genera and that species in *Oligosita* were assignable to both. The apparent polyphyletic nature of *Oligosita* led to a review of the entire tribe. The results presented here include a preliminary phylogenetic analysis which tests our initial hypothesis of generic grouping, a generic key, and a brief taxonomic summary of each genus.

The current classification of Trichogrammatidae proposed by Viggiani (1971, 1984) is based largely on male genitalia. Two subfamilies are recognized, each with two tribes (Trichogrammatinae: Trichogrammatini, Paracentrobiini; Oligositinae: Chaetostrichini, Oligositini). The genitalia of Oligositinae are reduced and modified to form a single tubular structure which lacks volsellae, parameres and a separate aedeagus (Fig. 10). The greatest modification occurs in the Oligositini where the anterodorsal aperture, the opening into which the ejaculatory duct enters, is extremely reduced in size (Fig. 11). Non-genitalic derived features supporting the monophyly of the tribe include black compound eyes and the single pair of setae on both the midlobe of the mesoscutum and the scutellum (Fig. 26).

The genera assigned to the Oligositini include *Chaetostrichella* Girault, *Doirania* Waterston, *Epoligosita* Girault, *Eteroligosita* Viggiani, *Hayatia* Viggiani, *Megaphragma* Timberlake, *Oligosita*, *Prestwichia* Lubbock, *Probrachista* Viggiani, *Prosoligosita* Hayat, *Pseudoligosita* Girault and *Sinepalpigramma* Viggiani and Pinto. *Pseudoligosita*, long treated as a junior synonym of *Oligosita* (Doutt and Viggiani 1968), is resurrected to house species removed from *Oligosita*.

The monotypic genus *Brachistagrapha* De Santis (1997), although considered related to *Chaetostrichella* when described is not an oligositine. We have examined the

holotype and paratype of *B. caudata* De Santis and find that the species belongs to the genus *Chaetogramma* Doutt (Trichogrammatini). It is very close to described species. We therefore treat *Brachistagrapha* as a junior synonym of *Chaetogramma* (**New synonymy**).

PHYLOGENETIC ANALYSIS

Taxa.—Phylogenetic analysis treats 15 oligositine OTUs. Included are *Chaetostrichella, Doirania, Epoligosita* (*Epoligosita*), *Epoligosita* (*Epoligositina*) Livingstone and Yacoob, *Eteroligosita, Hayatia, Megaphragma, Prestwichia, Prosoligosita, Pseudoligosita* and *Sinepalpigramma*. A single undescribed species of *Pseudoligosita*, sp. I, from Israel, is analyzed separately. Also separated are three groups of species which remain in *Oligosita*: *Oligosita*-C (= the Collina Group as defined by Nowicki 1936, and Viggiani 1976b), *Oligosita*-M (= the Minima Group as defined by Nowicki 1936, and Viggiani 1987), and a group of generalized *Oligosita* which differs from congeners in certain characters used in analysis but does not belong to either of the other assemblages (= *Oligosita*-G). With the exception of *Oligosita*-G, *Oligosita*-M and *Pseudoligosita* (see below), all groups analyzed are confidently hypothesized as monophyletic based on morphological synapomorphies. Characteristics of all assemblages and an indication of material studied are given in the generic synopses.

The oligositine genus *Probrachista* was excluded from analysis. It is known from females only, and the few specimens available are slide mounted precluding adequate examination of several features. *Pseudoligosita gerlingi* (Viggiani), a species differing considerably from congeners, also was excluded because of inadequate material (see below). In addition, we did not consider a small group of undescribed *Pseudoligosita* which are likely to be assigned to *Doirania* once males are discovered (also see below).

The genus *Uscana* is used as the outgroup for phylogenetic analysis. It was selected for the following reasons: 1) It is a generalized representative of the Chaetostrichini, the other tribe of Oligositinae. 2) The structure of its male genitalia deviates minimally from that of the Oligositini; the primary difference is the larger anterodorsal aperture (Fig. 10, also see Viggiani 1971). 3) Its antenna has four postanellar flagellomeres (Fig. 15), the maximum number found in the Oligositini. The inclusion of *Bloodiella* Nowicki, a chaetostrichine with antennal segment number and arrangement similar to most oligositines (see Doutt and Viggiani 1968), was precluded because of insufficient study material.

Characters.—Thirty-two binary and multistate morphological characters were coded for analysis; all were treated as unweighted and unordered. Autapomorphies associated with binary characters were not included, the exception being those characterizing the entire tribe (chars. 2, 4, 6, 28). Character selection focused largely on features without intragroup variation. All but two of the characters (chars. 9, 20) coded below are invariable within all OTUs. These two are entered as polymorphic.

The following characters were employed for analysis. The character matrix used is given in Table 1.

1. Distance from toruli to epistomal suture: subequal to clypeus length (0); distinctly greater than length of clypeus (1). The position of the toruli varies considerably in the family. In most genera they are in the more ventral position.

2. Eye color: reddish (0); black (1). Eye color is reddish in virtually all Trichogrammatidae; black eyes distinguish the Oligositini.

3. Funicular segment of antenna: distinctly separated from club segments (0) (Fig. 16); approximating club base, resulting in club appearing 4-segmented (1) (Fig. 20). Separating funicular from club

Table 1. Data matrix for the 32 characters used in the phylogenetic analysis. Polymorphisms indicated by letter 'a' (= 0/1).

Taxon	Characters																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Uscana	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Megaphragma	1	1	0	1	1	1	1	1	1	0	0	0	0	3	0	0	1	1	0	1	1	3	0	0	1	0	0	1	0	0	0	0
Prestwichia	1	1	1	1	1	1	1	1	1	0	0	0	0	3	0	1	1	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0
Sinepalpigramma	1	1	1	1	2	1	1	0	1	0	1	0	0	2	0	1	1	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0
E. (Epoligosita)	0	1	0	1	0	1	1	1	0	1	1	0	0	2	2	1	0	1	1	0	1	3	1	0	0	0	0	1	0	0	0	0
E. (Epoligositina)	0	1	0	1	0	1	1	1	0	1	1	0	?	3	2	0	0	1	1	1	1	3	1	0	0	0	0	1	0	0	0	0
Oligisita - M	1	1	0	1	0	1	1	1	0	0	1	0	0	2	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0
Oligosita - C	0	1	0	1	0	1	1	1	0	0	0	1	0	0	2	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Oligosita - G	1	1	0	1	0	1	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Pseudoligosita	0	1	0	1	0	1	0	0	a	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0
Pseudoligosita - I	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0
Prosoligosita	1	1	1	1	0	1	1	1	0	0	1	0	?	2	1	1	1	1	0	a	1	2	0	0	0	0	0	1	0	0	0	0
Doirania	0	1	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0
Chactostrichella	0	1	0	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0
Hayatia	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	2	2	1	2	0	1	1
Eteroligosita	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	2	2	1	2	0	1	1

segments often is arbitrary in chalcidoids. In most oligositines the single funicular segment is distinctly separated from the club. In some members of the tribe, as in *Uscana* (Fig. 15), it approaches the club rather closely. The difference between antennal structure in *Prosoligosita* (defined as having a 4-segmented club) and *Prestwichia* (with 1 funicular segment closely appressed to its 3-segmented club) is minimal. Deciding between the two character states as defined here, however, is relatively straightforward. Although there also is variation in antennal segment number in the tribe it was not incorporated into the analysis because of considerable intrageneric plasticity (e.g. in *Megaphragma* and *Epoligosita*).

4. Placoid sensilla on second postanellar antennal segment of female: present (0) (Fig. 15); absent (1) (Figs. 16–18, 20, 22). The absence of placoid sensilla on this segment characterizes females of all Oligositini. They are present in the outgroup and in several other genera.

5. Maxillary palp: present, well developed (0) (Fig. 23); present but reduced in size (1); absent (2) (Fig. 24). The maxillary palp in most Trichogrammatidae (state '0') consists of 1 or 2 distinct segments with 2–3 apical sensilla. In state '1' at least 1 terminal sensillum remains but the segment is reduced considerably in size.

6. Pairs of setae on the midlobe of the mesoscutum and scutellum: two (0), one (1). A single pair of setae on both the mesoscutal midlobe and scutellum characterizes all oligositine genera. Two pair on each is typical of most other trichogrammatid genera. In a few genera (e.g. *Pintoa*) there is a single pair on the midlobe but 2 pair on the scutellum.

7. Propodeal disk: not well differentiated, short, straplike, at most slightly produced posteriorly with an arcuate posterior margin, not distinctly longer than metanotum (0) (Fig. 29); distinct, produced posteriorly, often triangular or rectangular, distinctly longer than metanotum (1) (Figs. 26–28).

8. Propodeal and mesopleural surface: relatively smooth (0) (Fig. 31); subrugose or subrugulose (1) (Fig. 30). This character refers to the surface of the entire mesosoma but is best contrasted on the propodeum and pleural areas. In *Sinepalpigramma* (scored as '1') only the pleural areas are subrugose.

9. Propodeal spiracle: an anterior slit between spiracle and anterior margin of propodeum present (0); an anterior slit absent, propodeal spiracle surrounded by cuticle (1). It appears that an anterior slit occurs in most trichogrammatids. This feature is sometimes difficult to code because instead of a deep slit there is only a groove anterior to the spiracle. The distinction between '0' and '1' is especially problematic in slide mounted material. Both states occur in *Pseudoligosita*.

10. Subpropodeal lobe: absent (0); present (1) (Fig. 25). In *Epoligosita* (*Epoligosita*) and apparently *E.* (*Epoligositina*) there is a small auricular lobe subtending the propodeal disk. It is not clear if this structure is propodeal or associated with the first metasomal segment. We are not aware of this structure in any other trichogrammatid. Although best appreciated with the SEM, on well cleared slide-mounted specimens this lobe appears as a small triangle immediately behind the propodeal disk. The presence of this structure has been verified in numerous nominate *Epoligosita*. Our representation of *Epoligositina* is scanty (2 specimens), and the consistent presence of a lobe in this subgenus remains questionable.

11. Mesophragma: evenly rounded, entire apically (0); bilobed apically (1). The apex of the mesophragma is apically bilobed in most trichogrammatid genera.

12. Mesopleural suture: present (0) (Fig. 30); absent (1) (Fig. 31). This character is not easy to appreciate in card- or slide-mounted specimens. In addition to the difficulty attributable to body size, the presence of an internal pleural ridge can be misinterpreted as a pleural suture. In several taxa a distinct line, appearing to be the pleural suture, extends from the base of the mesocoxa to the fore wing base. SEM examination however showed no external evidence of a suture in these specimens. A pleural suture, evidenced by a distinct external line or groove, characterizes most genera of trichogrammatids.

13. Mesosternum: without transepisternal sulci (0) (Fig. 32); with transepisternal sulci (1) (Fig. 33). In the Oligositini the presence of transepisternal sulci (*sensu* Gibson 1989) is correlated with the absence of the mesopleural suture. However, presence or absence of these sulci are included here as distinct from character 12 because the correlation does not occur in all trichogrammatid genera (e.g. in *Lathromeroidea* [unpubl. obs.]). We are not yet aware of transepisternal sulci in any non-oligositine taxon of Trichogrammatidae.

14. Maximum fringe length of fore wing to greatest fore wing width: 0.2 or less (0); 0.3–0.7 (1); 0.9–1.5 (2); >2.0 (3). This character was coded after recording the fringe/wing width ratio for a range of representatives of each OTU. Although there is a general difference in fringe length among taxa it is almost certain that the gaps between codes would be bridged with additional sampling. Because fringe length is roughly correlated with wing width (see Figs. 2–7), the latter was not employed as a separate character.

15. Fore wing disk setation density: dense to moderately dense (0) (Figs. 4–7); relatively sparse (1) (Fig. 3); without setae on disk (2) (Fig. 2). This character was quantified for exemplars of each OTU as follows: across widest aspect of wing, distance in mm taken between 4–6 setae from anterior to posterior margin of wing and the mean distance calculated; distances were measured from a seta to the nearest seta posteriorly. If no closest seta existed posteriorly or setation consisted of only a single row of setae (e.g. *Megaphragma*), then distance taken to wing margin(s). For state '0', intersetal distance ranged from 0.008–0.016 mm; for state '1', it ranged from 0.023–0.029 mm.

16. Basal sensilla on fore wing (immediately anterior to retinaculum on dorsal surface): absent (0); present (1). These refer to the presence of a small field of minute unsocketed structures at the base of the wing (illustrated in Pinto 2004). In some

taxa (e.g. *Oligosita*-C) they are acuminate apically; in others (e.g. *Pseudoligosita*) they commonly are clavate. Although these structures also occur in certain non-oligositines (e.g. the Paracentrobiini), they appear to be absent in the majority of genera, including the more primitive groups (i.e. members of the Trichogrammatini).

17. Posterior margin of fore wing: without an abrupt shift in outline at apex of retinaculum (0) (Fig. 3); with an abrupt shift in outline immediately beyond apex of retinaculum, resulting in wing width being slightly narrower at this point than at apex of retinaculum itself (1) (Fig. 4). Although state '1' seems to be associated with narrow wings the correlation is not perfect by any means. For example, several taxa with quite narrow wings (e.g. *Epoligosita, Oligosita*-C) are exceptions.

18. Premarginal vein with apical seta: present (0); absent (1). A basal and apical seta occur on the premarginal vein in most Trichogrammatidae.

19. Premarginal vein at junction with marginal vein: of similar width to marginal vein (0) (Figs. 3–7); abruptly wider than marginal vein (1) (Fig. 2).

20. Number of campaniform sensilla at apex of premarginal vein: two (0); one (1). Two campaniform sensilla mark the apex of the premarginal vein in trichogrammatids. In some taxa only a single sensillum is obvious. This reduction tends to be more common in groups with smaller body size. *Prosoligosita* possesses either 1 or 2 sensilla.

21. Stigma: subtriangular or subrectangular, connected to marginal vein with a distinct and narrow stigmal vein (0); subcircular or suboval, sessile to marginal vein or connected by a slight constriction only (1).

22. Number of rows of setae on disk of hind wing: three (0); two (1); one (2); zero (without setae) (3). The more primitive groups of Trichogrammatidae tend to have more dense hind wing setation. Although roughly related to wing width, this correlation has several exceptions.

23. Mesotarsus: shorter than mesotibia (0); distinctly longer than mesotibia (1).

24. Metasomal terga: surface of all more or less similar entire length (0); at least the anterior-most 3 with posterior section (half or more) striate, with longitudinal cuticular stripes contrasting with evenly sclerotized anterior section of tergum (1) (Figs. 29, 31). The striations characterizing state '1' are usually distinct and easily seen. However in some species they are exceedingly faint and visible only under high magnification of well-cleared specimens, or with SEM. The anterior-most sterna may be longitudinally striate as well. Bipartite metasomal terga and sterna are unknown outside of the Oligositini.

25. Metasomal tergum VII: with spiracles (0); without spiracles (1). The absence of spiracles on the 7th metasomal tergum is an uncommon feature in trichogrammatids. We are aware of this trait only in the Oligositini.

26. Metasomal tergum VII in males: not noticeably modified (0); darker than preceeding terga and presumably with a thicker cuticle (Fig. 13), surface sometimes modified as well (asperous or subrugulose) (1); with a small reticulate patch anteromedially (2). It is not clear how state '2' relates to state '1' except that it represents a modification of the same tergum.

27. Metasomal venter of male: normal, without medial projections (0); with a single posteriorly directed projection (1) (Fig. 35); with 2 or 3 narrow medial projections (2). States '1' and '2' represent unique features in the Trichogrammatidae. In state '1' there is a single projection. The structure is subquadrate in *Doirania leefsmani* Waterston (see Pinto 2004). It is elongate and linguiform in *Pseudoligosita* and *Chaetostrichella* (Fig. 35) and apparently also in *Doirania elegans* Pinto although shriveling of the single male available for SEM preparation precludes adequate description. In *Pseudoligosita* at least, the medial projec-

tion appears to be an extension of sternum IV (Figs. 13, 35). It is poorly sclerotized and visible but difficult to discern in slide-mounted specimens. In state '2' there are at least 2 very narrow, elongate medial sternal projections. Viggiani (1976b: Tbl. II, Fig. 4) shows three in *Eteroligosita tamaricis* Viggiani. We observe at least 2 in *Hayatia*. The anteriormost projection in state '2' is presumably homologous to that in state '1'. The function of these unique structures is unknown.

28. Male genitalia: with relatively large anterodorsal aperture (0) (Fig. 10); with reduced anterodorsal aperture (1) (Figs. 11, 12, 36, 37). The reduced anterodorsal aperture is a defining feature of the Oligositini.

29. Male genitalia: a simple tube with, at most, 2 longitudinal, anteriorly directed apodemes at base (0) (Fig. 11); variously modified at apex but with 2 posteriorly directed apodemes (1) (Figs. 12, 36); of a highly modified type (2).

As indicated, the male genitalia in the Oligositinae are considerably reduced and modified relative to the generalized chalcidoid condition. In the Chaetostrichini all genitalic parts are consolidated into a single tube but a relatively large anterodorsal aperture remains (Fig. 10). In the Oligositina and in at least *Doirania* as well as a few species of *Pseudoligosita* of the Eteroligositina (state '0'), this condition is retained except the aperture becomes considerably reduced with some basal sclerotization associated with the rim of the aperture remaining (Fig. 11). State '1' represents a modification primarily of basal structure. The anterodorsal aperture opens anteriorly instead of dorsally and the sclerotization surrounding the aperture has 2 elongate, posteriorly directed arms or apodemes which subtend the shaft of the genitalia and are attached to the sternal plate beneath (apparently sternum VII, see Figs. 14, 36, 37). These apodemes also may continue anteriorly a short distance. The genitalia are strongly arched dorsally as is the sternal plate beneath (Figs. 14, 37). During genital exsertion the base of the genitalia does not move relative to its sternum. Instead the strongly arched sternum beneath is flattened out which, owing to its attachment to the genital base, swings the strongly curved genital shaft ventrally and out of the body between divided sternal plates. The mechanism causing genital exsertion is unknown but the genitalia can easily be forced out in specimens softened in alcoholic KOH by gently squeezing the metasoma, suggesting that hydrostatic pressure may be involved.

The genitalia in state '0' also appear to be stationary at the base. In state '0' taxa the genitalia also exit the body between the strongly incised (or completely divided?) last sternum (Fig. 34). The genitalia of *Pseudoligosita* I may represent an intermediate condition between states '0' and '1'. The posteriorly directed apodemes, while apparently present, are very short, and the genitalia are not strongly curved. Sternal modifications also are absent in this species.

Whereas states '0' and '1' represent relatively straightforward modifications of the generalized chaetostrichine genitalia, state '2', characterizing *Hayatia* and *Eteroligosita*, is not so easily understood. In these genera the genitalia are modified into an exceptionally elongate serpentine structure (Fig. 38), which is folded upon itself when at rest within the metasoma (Fig. 39). The anterodorsal aperture is very small but its orientation is not clear (see Viggiani 1976a).

30. Male genitalia: slightly curved ventrally (0) (Figs. 11, 34); strongly curved ventrally (1) (Figs. 12–14, 37).

31. Genitalia entire at apex (0) (Fig. 34); bifid at apex (1). The apex of the genitalia (= aedeagus) in *Pseudoligosita*, *Chaetostrichella*, *Hayatia* and *Eteroligosita* is bifid, however in the former 2 genera it is only slightly so (Fig. 36) compared to the condition in *Hyatia* and *Eteroligosita* (Fig. 38).

Table 2. List of synapomorphies for clades in Figure 1.

Clade	Defining synapomorphies[1]
A. Oligositini	2, 4, 6, 16[2], 22[3], 28
B. Eteroligositina	8, 12, 13, 24
C. (*Pseudoligosita* - *Chaetostrichella*)	9, 26, 27, 29, 30, 31
D. (*Hayatia* - *Eteroligosita*)	26 (0-2), 27 (0-2), 29 (0-2), 31, 32
E. Oligositina	7, 14, 21
F. (*Oligosita* C - *Prestwichia*)	14 (1-2), 15[4]
G. (*Epoligosita* - *Prestwichia*)	18
H. (*Epoligosita* - *E.* [*Epoligositina*])	10, 15 (1-2), 19, 22 (1-2), 23
I. (*Oligosita* M - *Prestwichia*)	1, 17, 20
J. (*Prosoligosita* - *Prestwichia*)	3[5]
K. (*Sinepalpigrauma* - *Prestwichia*)	5, 9, 15 (1-0), 25
L. (*Megaphragma* - *Prestwichia*)	11, 14 (2-3)

[1] Characters listed assume advance from 0 to 1 unless indicated in parentheses. Character explanations given in text.
[2] Reversed in *E.* (*Epoligositina*) and *Megaphragma*.
[3] Reversed in *Hayatia*.
[4] Reversed in clade K.
[5] Reversed in *Megaphragma*.

32. Third valvulae of ovipositor: normal in width, not abruptly narrower than 2nd valvulifer (inner plates) (0); abruptly narrower than apex of 2nd valvulae, bristle-like (1) (see Viggiani 1996).

Analysis.—Phylogenetic analysis of the Oligositini employed maximum parsimony using PAUP* 4.0b10 (Swofford 2002). The branch and bound tree-searching algorithm was employed. Unweighted analysis was followed by successive approximations character weighting (Farris 1969) using the rescaled consistency index (maximum value) and a base weight of 1000. Summary statistics represent values after characters were reweighted at unity following successive approximations. Results were compared by generating strict consensus cladograms following both unweighted and weighted runs. Selected cladograms were transported to MacClade 4.0 (Maddison and Maddison 2003) for character analysis. Bootstrap values (nreps = 1000) were calculated to show level of clade support.

Results.—Branch and bound analysis resulted in five trees of 59 steps (CI = 0.70; RI = 0.82). Successive approximations weighting produced four trees with the same tree statistics. The strict consensus tree from the weighted analysis is presented in Fig. 1. This consensus tree is the same as that produced by unweighted analysis except for the relationship between *Pseudoligosita* and *Chaetostrichella*. Successive approximations hypothesizes a sister group relationship, whereas unweighted analysis leaves their relationship within the *Doirania-Eteroligosita* clade unresolved.

Table 2 lists the synapomorphies for the various clades (A–L) indicated in Fig. 1. Analysis justifies dividing the tribe into two subtribes, the Oligositina and the Eteroligositina. The tribe Oligositini (clade A) is supported by several derived features. There also is robust support for distinguishing the Eteroligositina (clade B) from remaining members of the tribe. The three features supporting the Oligositina (clade E) are somewhat subjective, quantitative and difficult to code. The monophyly of this subtribe remains questionable, relatively high bootstrap support notwithstanding. Although more convincingly monophyletic, relationships are poorly resolved within the Eteroligositina

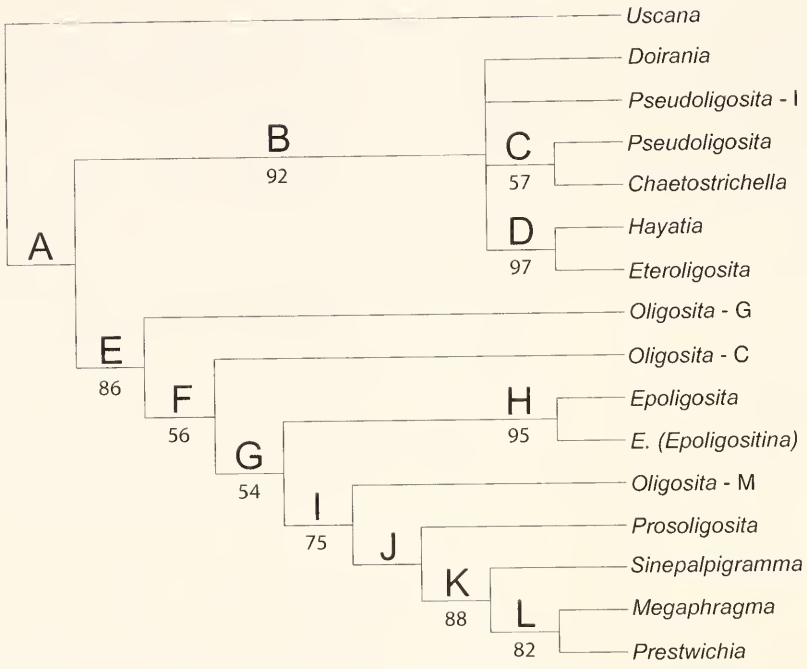
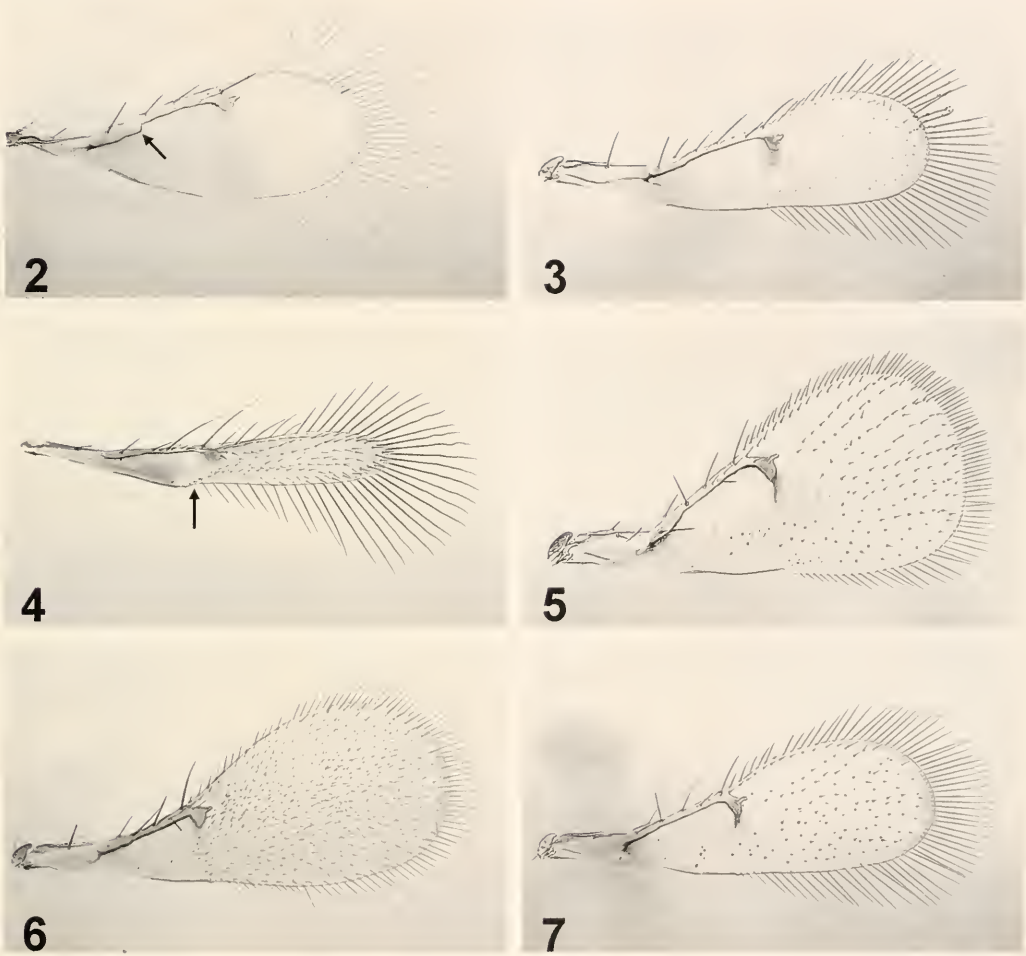


Fig. 1. Strict consensus of four cladograms after successive approximations weighting based on character data in Table 1. Tree length = 59; consistency index = 0.70; retention index = 0.82. Bootstrap values (if > 50%) are placed below the branches. Synapomorphic characters for clades A–L given in Table 2. The unweighted consensus tree (same statistics) differs only in that the sister group relationship between *Pseudoligosita* and *Chaetostrichella* (clade C) is not supported.

(clade B). The sister group relationship between *Hayatia* and *Eteroligosita* (clade D) has considerable support, but other relationships require additional input and taxon sampling. *Pseudoligosita* and *Chaetostrichella* are likely closely related (clade C). We are aware of no derived features defining *Pseudoligosita* not also shared with *Chaetostrichella* and it is possible that the latter simply represents a derived element of *Pseudoligosita*. Given the lack of derived features, *Pseudoligosita*-I is not given generic status at this time. *Probrachista* was not available for analysis but it clearly belongs to the Eteroligositina and appears closest to *Chaetostrichella* (see below).

Although the Oligositina is questionably monophyletic, there is strong support for two clades within the subtribe. Clade H [(*Epoligosita-E.* (*Epoligositina*)] is defined by several characters and is compatible with treatment of the two taxa as congeneric. Clade K is based on four characters including the loss of the posterior metasomal spiracles, as far as we know, a unique feature in the family. Most of the remaining clades are questionable and require testing by additional evidence particularly since several of the apomorphic features represent reductions and perhaps are correlated with small body size. Figure 1 shows that *Oligosita* as herein defined remains polyphyletic even with the removal of *Pseudoligosita*.

Discussion.—The preliminary nature of this study prevents us from making all taxonomic changes suggested by the results. We consider the primary purposes of our analysis to be providing an estimate of the coarse phylogenetic topology of the tribe and determining if our initial hypothesis of *Oligosita* polyphyly could be supported. We believe the value of phylogenetic analysis as not only justifying



Figs. 2–7. Fore wings of Oligositini genera. 2, *Epoligosita* (arrow to abruptly wider premarginal vein). 3, *Oligosita*-C species. 4, *Prestwichia* (arrow to abruptly narrower margin of wing apical to retinaculum. 5, *Eteroligosita*. 6, *Probrachista*. 7, *Pseudoligosita*.

taxonomic modification but also as identifying problems requiring additional input before taxonomic resolution. Thus, we feel the character evidence is adequate to support dividing the Oligositini into two subtribes and removing several *Oligosita* and placing them in a resurrected *Pseudoligosita* belonging to the other subtribe. However, we hesitate dividing *Oligosita* further, notwithstanding its continued depiction as polyphyletic. This is an enormously diverse and character-poor genus. Perhaps the majority of species await discovery and description. At least one of the subgroups incorporated in the study (*Oligosita*-G) is a heterogeneous assemblage without well-defined features. Also, all implied relationships involving sections of *Oligosita* in Figure 1 either have minimal character support, and/or are based on character loss or qualitative traits especially prone to subjective coding (Table 2). This also is reflected by minimal bootstrap support for these clades. Clearly, greater representation and an in-depth intrageneric character analysis is required before proposing additional taxonomic modifications.

KEY TO THE GENERA OF OLIGOSITINI

1. Metasoma with terga uniformly sclerotized their entire length. Propodeal disk usually distinctly longer than metanotum at midline (Figs. 26–28). Propodeum and mesosomal pleural areas usually subrugulose (Figs. 27, 30). Mesopleuron with pleural suture (Fig. 30); transepisternal sulci absent (Fig. 32) ..... (Oligositina) 2
– Metasoma with at least the three anterior terga longitudinally striate in posterior section, anterior section uniformly sclerotized (Figs. 29, 31). Propodeal disk usually only slightly longer than metanotum (Fig. 29). Propodeum and mesosomal pleural areas smooth (Figs. 29, 31). Mesopleuron without pleural suture (Fig. 31); transepisternal sulci present (Fig. 33) ..... (Eteroligositina) 8

2. Fore wing disk entirely glabrous (rarely with one or two setae) (Fig. 2). Mesosoma with a small subtriangular lobe arising beneath propodeal disk (Fig. 25). Mesotarsus elongate, distinctly longer than mesotibia 3
– Fore wing disk sparsely to moderately densely setose (Figs. 3, 4). Mesosoma without a small subtriangular lobe arising beneath propodeum. Mesotarsus not longer than mesotibia 4

3. Antenna with a distinct funicular segment (Fig. 16) ..... ***Epoligosita* (*Epoligosita*)**
– Antenna without a distinct funicular segment ..... ***Epoligosita* (*Epoligositina*)**

4. Maxillary palps absent (Fig. 24). Antenna without linear placoid sensilla on surface of club (males unknown) ..... *Sinepalpigramma*
– Maxillary palps present. Antenna with linear placoid sensilla on surface of last two segments of club 5

5. Antenna with four postanellar segments, including a single funicular segment distinctly separated from a three-segmented club (Fig. 18). Mesophragma notched apically. Many species with a clavate terminal process (= modified placoid sensilla) at apex of club in females (Fig. 19) ..... ***Oligosita***
– Antenna with three or four postanellar segments, if with four then the funicular segment closely associated with club (Fig. 20). Mesophragma not notched apically. Without a clavate terminal process on apex of club of females 6

6. Fore wing of moderate width, ca. 3× as long as wide (as in Fig. 3) ..... ***Prosoligosita***
– Fore wing extremely narrow, ca. 7× as long as wide (Fig. 4) 7

7. Antenna with three postanellar segments (Fig. 17). Fore wing sparsely setose with only one or two rows of setae on disk ..... ***Megaphragma***
– Antenna with four postanellar segments (Fig. 20). Fore wing densely setose (Fig. 4) .... ***Prestwichia***

8. Antennal club one segmented 9
– Antennal club two or three segmented 10

9. Funicular segment longer than wide. Ovipositor elongate, extending well beyond apex of metasoma. Male genitalia with posteriorly directed apodemes at base (as in Fig. 12) ..... ***Chaetostrichella***
– Funicular segment wider than long. Ovipositor relatively short, not extending beyond apex of metasoma or only slightly so. Male genitalia without posteriorly directed apodemes (as in Fig. 11) ..... ***Doirania***

10. First club segment somewhat disassociated from segment II, appearing as a second funicular segment (Fig. 9). Fore wing densely setose (Fig. 6). Ovipositor extending well beyond apex of metasoma ..... ***Probrachista***
– First club segment closely appressed to second, distinct from funicular segment (Fig. 22).

Fore wing variable but usually not densely setose (as in Figs. 5, 7). Ovipositor variable in length but rarely extending more than slightly beyond apex of metasoma 11

11. Ovipositor with 3rd valvulae bristlelike, abruptly narrower than 2nd valvulifer (inner plates). Last sternum of male extending posteriorly well beyond apex of last tergum (Fig. 39). Genitalia extremely long (Fig. 38), folded upon itself when not exserted (Fig. 39), strongly bifurcate apically (Fig. 38) 12
– Ovipositor with 3rd valvulae normal, not bristlelike, not abruptly narrower than 2nd valvulifer. Last sternum of male not extending beyond apex of last tergum (Fig. 13). Genitalia of normal length, only slightly bifurcate (Fig. 36) ..... ***Pseudoligosita***

12. Male antenna (Fig. 21) with placoid sensilla on all three club segments, those on C3 relatively narrow; funicular segment short, wider than long. Hind wing with three setal tracks ..... ***Hayatia***
– Male antenna (Fig. 8) without placoid sensilla on first club segment, second and third club segments with extremely wide placoid sensilla; funicular segment about as long as wide. Hind wing with two setal tracks ..... ***Eteroligosita***

Subtribe Oligositina Walker

Diagnosis: Antenna with funicle distinct from club or closely appressed to it. Fore wings relatively narrow to very narrow, with disk glabrous to moderately densely setose; stigma subcircular or suboval, usually sessile to marginal vein or connected by a slight constriction; dorsum and sides of mesosoma usually subrugulose; propodeal disk typically subtriangular or subrectangular, considerably longer than metanotum; pleural suture present on mesopleuron; mesosternum without transepisternal sulci. All metasomal terga uniformly sclerotized their entire length; metasomal tergum II (1st visible) often longitudinally rilled medially (Figs. 26, 27). Male genitalia simple, consisting of a single tubular structure and, at most, 2 anteriorly directed apodemes at base.

Epoligosita Girault

Paroligosita Girault and Dodd, in Girault 1915: 145 (as subgenus of *Oligosita*). Type species: *Paroligosita biclavata* Girault and Dodd, by original designation.

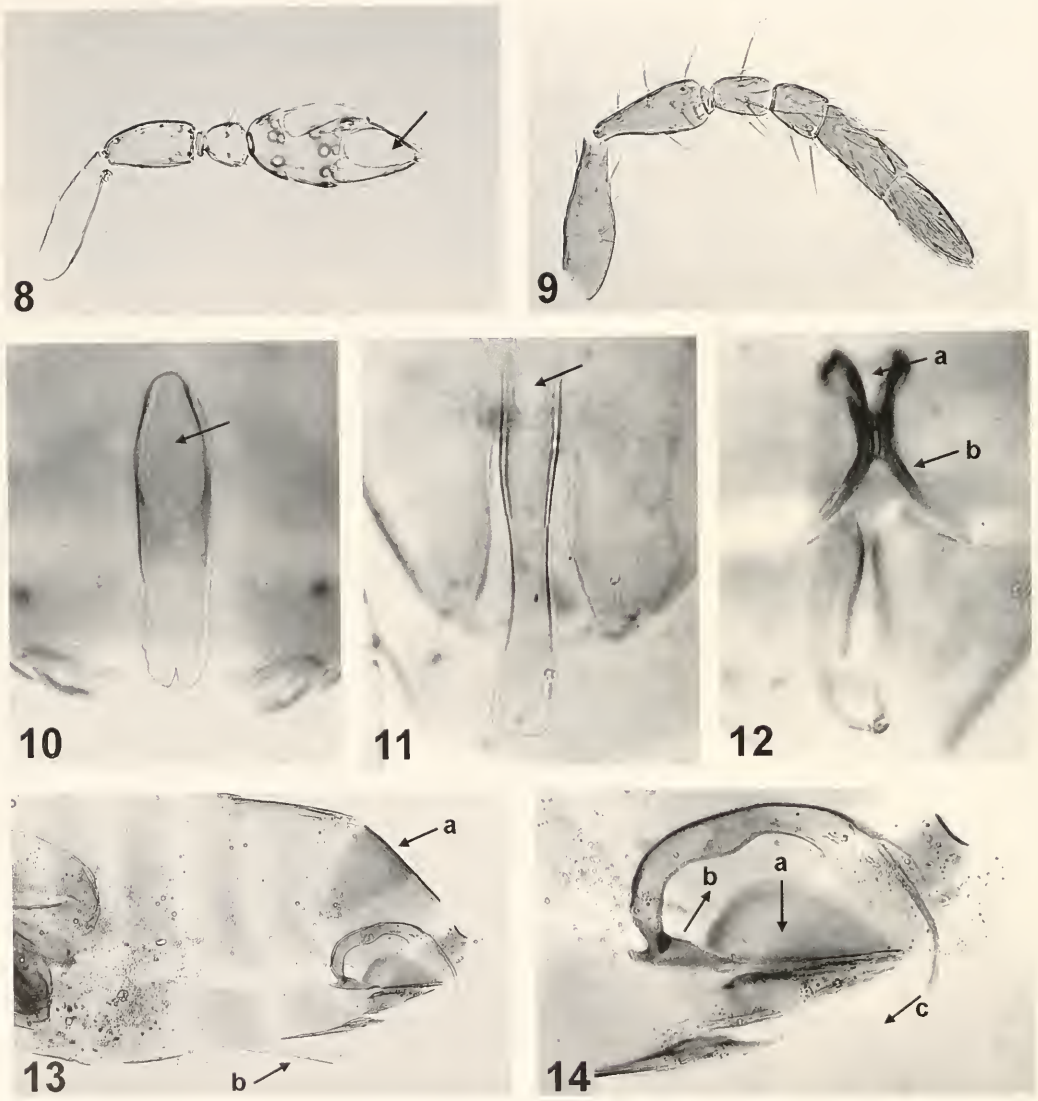
Epoligosita Girault 1916: 206 (n. n. for *Paroligosita* Girault and Dodd, *nec* Kurdjumov 1911) (as genus).

Epoligositina Livingstone and Yacoob 1983: 214 (as subgenus). Type species: *Epoligosita* (*Epoligositina*) *dulitiae* Livingstone and Yacoob, by original designation. Lin 1990 (as genus). **Renewed status as subgenus.**

Diagnosis.—Antenna with 1 funicular segment present or absent, and a 1–2 (rarely 3) segmented club; sutures subdividing club often incomplete; funicle, when present, distinct from club. Tarsi elongate, those of fore and middle leg longer than their respective tibia; tarsomere I of mesotarsus especially elongate in most species. Fore wing ca. 3–4× as long as wide, widest near level of stigma, gradually narrowing to apex; fringe setae elongate, length varying from subequal to wing width to ca. 2× greater; disk bare, with at most 1 or 2 setae; entire posterior margin evenly arcuate; premarginal vein abruptly wider than marginal vein at junction. Propodeal disk subtended by a small subtriangular lobe.

The shape of the fore wing (widest at the stigma, narrowing to apex), the virtual absence of setae on the fore wing disk, the presence of the triangular lobe subtending the propodeal disk, and the elongate tarsi provide the best separation of *Epoligosita* from other genera.

Comments.—There are 22 described species of *Epoligosita*. We recognize two subgenera, the nominate subgenus with 17 species and *Epoligositina* with five. The for-



Figs. 8–14. 8–9, antennae. 8, *Eteroligosita* (medial; arrow to greatly enlarged placoid sensillum on last club segment). 9, *Probrachista*. 10–14, male genitalia. 10, *Uscana semifumipennis* Girault (dorsal; arrow to relatively large anterodorsal aperture). 11, *Oligosita* (dorsal; arrow to reduced anterodorsal aperture). 12, *Pseudoligosita* (ventral; arrow-a to reduced anterodorsal aperture, arrow-b to posteriorly directed apodemes at base of genitalia). 13, *Pseudoligosita* (lateral of metasoma; arrow-a to modified metasomal tergum VII above genitalia, arrow-b to medial projection of sternum IV beneath genitalia. 14, *Pseudoligosita* (as 13, higher magnification of genitalia and associated sterna). Arrows illustrate unique process of genitalia eversion: domed shape sternum VII is brought down and flattened (direction indicated by arrow-a); the flattening of sternum VII rocks base of genitalia forward (direction indicated by arrow-b) thus swinging the genitalia out of body and forward (direction indicated by arrow-c).

mer, although uncommonly collected, is known from all major regions of the world. *Epoligositina* occurs in Asia (India, China, Japan), and we have examined a single female of an apparently consubgeneric species from Somalia.

Epoligositina was described as a subgenus of *Epoligosita* by Livingstone and Ya-

coob (1983), distinguished by the lack of a funicular segment and more extensive fumation in the fore wing. The group was elevated to genus by Lin (1990). Considering the variation in antennal segment number among obviously related species of Oligositini we do not feel separation at the generic level is warranted. Subgeneric status also could be questioned, but we believe it appropriate considering the limited material of *Epoligositina* available for this study.

As indicated, there is considerable variation in antennal formula in *Epoligosita*. In addition to the presence or absence of a funicle, club structure also varies. In most species the club is one or two segmented; in some it is incompletely two or three segmented; and in a male of an undescribed species from New Guinea (female unknown) it is clearly three segmented. Thus, in the New Guinea species the antennal formula is exactly the same as in *Oligosita* and many other oligositines (one distinct funicular segment, three segmented club). This suggests that reduction in segmentation occurred after the origin of the genus.

Both subgenera of *Epoligosita* are known to attack eggs of Cicadellidae (Livingstone and Yacoob 1983, Viggiani 1985, Pinto and Viggiani 1987).

Material from throughout the range of *Epoligosita* (*Epoligosita*) was examined. Only two specimens representing two species of *E.* (*Epoligositina*) were available.

Megaphragma Timberlake

Megaphragma Timberlake 1923: 412. Type species: *Megaphragma mymaripenne* Timberlake, by original designation.

Sethosiella Kryger 1932: 38. Type species: *Sethosiella priesneri* Kryger, by original designation.

Paramegaphragma Lin 1992: 133. Type species: *Paramegaphragma stenopterum* Lin, by original designation.

Diagnosis.—Extremely small, body length less than 0.3 mm. Antenna with 0–1 funicular segments and 2–3 club segments; if funicle present, club with 2 segments; if funicle absent, club with 2 or 3 segments. Fore wing extremely narrow, strapshaped, ca. 7× as long as wide, with retinacular margin distinctly arcuate; fringe setal length ca. 5× greatest wing width; number of setae on disk few, varying from 0 to several arranged in 1 or 2 setal lines.

The minute body size (< 0.3 mm), and the exceptionally narrow, sparsely setose fore wing with its extremely long fringe setae separate *Megaphragma* from all other Oligositina.

Comments.—*Megaphragma* includes 15 species. Of the synonyms, *Sethosiella* was described by Kryger (1932) without any indication that he was aware of Timberlake's earlier description of *Megaphragma*. *Paramegaphragma* was described by Lin (1992) for species without a funicle and only two club segments. Its synonymy was proposed by Delvare (1993).

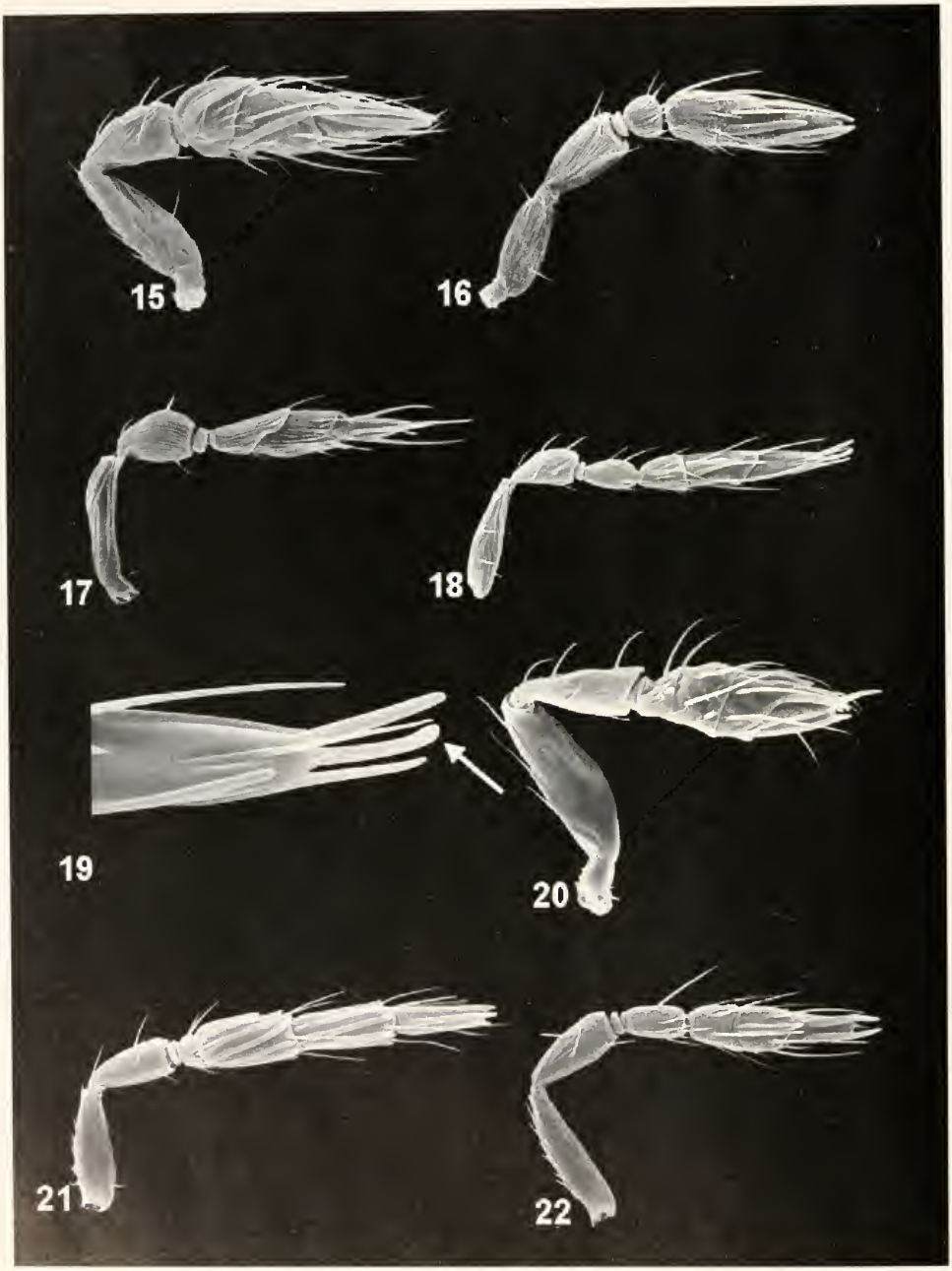
The species can be divided into three informal groups: (a) those with a funicle and a two-segmented club (*mymaripenne*, *analphitanum* Viggiani, *decohaetum* Lin, *polychaetum* Lin, *maguiclava* Yousuf and Shafee, *longiciliatum* Subba Rao, *priesneri*, and *anomalifuniculi* Yuan and Lou); (b) those without a funicle and a three-segmented club (*striatum* Viggiani, *aligarhensis* Yousuf and Shafee, and *ghesquierei* Nowicki); and (c) those without a funicle and a two-segmented club (*caribea* Delvare, *macrostigmum* Lin and *stenopterum* Lin). A revisionary study is required to determine if these represent natural groups.

Megaphragma is known from all biogeographic regions. Thysanoptera eggs are commonly recorded as hosts (Lin 1994).

We have examined several species of *Megaphragma* from all regions, including representatives of the three informal groups indicated.

Prestwichia Lubbock

Prestwichia Lubbock 1864: 140. Type species: *Prestwichia aquatica* Lubbock, by monotypy.



Figs. 15–22. Antennae. 15, *Uscana semifumipennis* (lateral, ♀). 16, *Epoligosita* (lateral, ♀). 17, *Megaphragma striatus* (lateral, ♀). 18, *Oligosita* (Collina Group) (medial, ♀). 19, same as Fig. 18, detail (arrow to clavate placoid sensillum at apex of club). 20, *Prestwichia* (lateral, ♀). 21, *Hayatia* (medial, ♂). 22, *Pseudoligosita* (lateral, ♀).

Austromicron Tillyard 1926: 279. Type species: *Austromicron zygopterorum* Tillyard, by original designation.

Diagnosis. Antenna with 1 funicular segment and 3 club segments; funicular segment closely associated with club. Mesosoma with dorsal surface distinctly reticulate. Propodeal disk distinct, elongate, subtrapezoidal. Fore wing very narrow, rounded apically, ca. 7× as long as wide; fringe setae 2.5–3× greatest wing width; retinacular margin moderately arcuate; disk densely setose at apical half. First tergum of metasoma with a rhomboidal-shaped platform at center. Males often wingless.

The characteristics of the fore wing (extremely narrow but densely setose), the close association of the funicle with the club, and absence of apical metasomal spiracles separate this genus from all other Oligositina. The rhomboidal-shaped platform at the center of the first visible metasomal tergum (Fig. 28) may be another distinguishing feature but its presence has not been verified in all species.

Comments.—Prestwichia includes five described species. The Australian *P. zygopterorum* was placed in its own genus (*Austromicron*) by Tillyard (1926) based on relatively minor traits, including fully alate males and a shorter, non-protruded ovipositor. The synonymy was recognized by Doutt and Viggiani (1968).

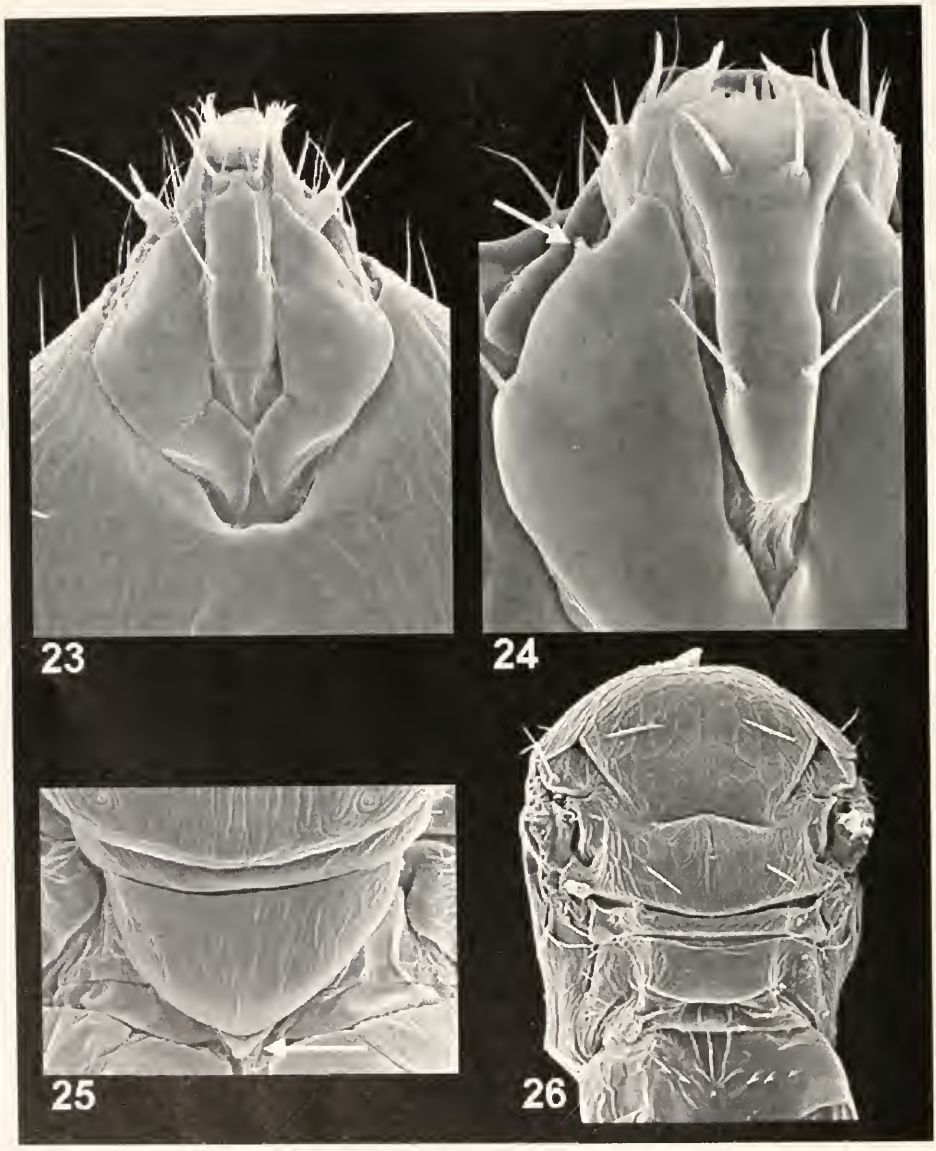
Described species of this uncommonly collected genus occur in Europe, Asia and Australia. It also has been collected from Africa (Ivory Coast) and North America (Florida) (unpubl.). It has yet to be taken in the Neotropics. *Prestwichia* has been recorded parasitizing eggs of a variety of aquatic Coleoptera, Hemiptera, and Odonata (Fursov 1995). We have examined described (*P. aquatica, P. zygopterorum*) and undescribed species from all areas of distribution.

Prosoligosita Hayat and Husain

Prosoligosita Hayat and Husain 1981: 81. Type species: *Prosoligosita perplexa* Hayat and Husain 1981, by original designation.

Diagnosis.—Antenna with a 4-segmented club; a distinct funicle absent; C4 longest of club segments and extremely narrow in female (> 3× as long as wide), C2 the shortest; placoid sensilla present on C1, C3 and C4 in both sexes, absent from C2 (i.e., from 2nd postanellar segment as in all oligositines). Fore wing almost 3× as long as wide; fringe setae almost as long to somewhat longer than maximum wing width (but not as long as twice maximum width); retinacular margin distinctly arcuate relative to remainder of posterior wing margin; stigma constricted at junction with marginal vein; disk sparsely setose with setae arranged in ca. 7 well-separated lines. The apparently 4-segmented club combined with the elongate and exceptionally narrow last club segment in females, the presence of a linear placoid sensillum on the 1st postanellar antennal segment, and the occurrence of apical metasomal spiracles separate *Prosoligosita* from other members of its subtribe.

Comments.—Prosoligosita was described from three females of a single species from India. A second Indian species, *P. meerutensis*, described by Yousuf and Shafee (1993) is known only from its unique type female. The only material of this genus discovered since these original descriptions includes a single male from Bangalore, India, a female from Sarawak, and a second female from Sulawesi. These three specimens are the only ones we have examined of this genus. The male is likely conspecific to *P. perplexa*; the females cannot confidently be placed to species but appear to be different yet close to *P. perplexa*. The male of *Prosoligosita* was not known previously. Its antennal features are similar to those of the female except the terminal club segment is not as elon-



Figs. 23–26. 23–24, ventral of head showing maxillae. 23, *Oligosita* (with 1-segmented maxillary palps). 24, *Sinepalpigramma longiciliatum* (arrow to appendicular remnant of maxillary palp). 25, *Epoligosita*, propodeal disk (arrow to subpropodeal lobe). 26, *Oligosita* (Minima Group), mesosoma and base of metasoma (dorsal).

gate (ca. 2× as long as wide); the genitalia are typical for the Oligositina.

The distinct four-segmented club appears to render this genus unique in the Oligositini. However in *Prestwichia* and *Sinepalpigramma*, the funicular segment closely approaches the club; it is only somewhat more closely appressed to the apical three flagellar segments in *Prosoligosita*, a minor difference at best. *Prosoligosita* also is distinguished by the presence of a linear placoid sensillum on the first postanellar segment in both sexes (= C1 in this genus). The only other occurrence of this trait in the tribe that we are aware of is in a few species of apparently unde-

scribed Australian *Oligosita* which have a linear placoid on the funicular segment.

Sinepalpigramma Viggiani and Pinto

Sinepalpigramma Viggiani and Pinto (2003). Type species: *Sinepalpigramma longiciliatum* Viggiani and Pinto, by original designation (type examined).

Diagnosis.—Antenna with a single funicular segment and a 3-segmented club; funicle closely associated with 1st club segment; antenna completely without linear placoid sensilla on surface and with only a single type of seta-like structure on flagellum. Females without maxillary palps. Surface of mesoscutum and scutellum extremely smooth, without any indication of reticulae.

Sinepalpigramma is perhaps the most easily recognized genus of Oligositini. The absence of maxillary palps is unique in the family. Antennal structure, the absence of antennal placoid sensilla, and the smooth mesosomal dorsum also are distinctive for the tribe.

Comments.—A clear male association is unknown. A single, poorly prepared male from Costa Rica may belong here. Character 29 (features of male genitalia) was coded for *Sinepalpigramma* based on this male. There are two described species. The genus occurs from central Mexico south to Argentina. Hosts are unknown.

Oligosita Walker

Oligosita Walker 1851: 212. Type species: *Oligosita collina* Walker, by monotypy.

Westwoodella Ashmead 1904: 359. Type species: *Oligosita subfasciata* Westwood, by original designation. Syntypes examined.

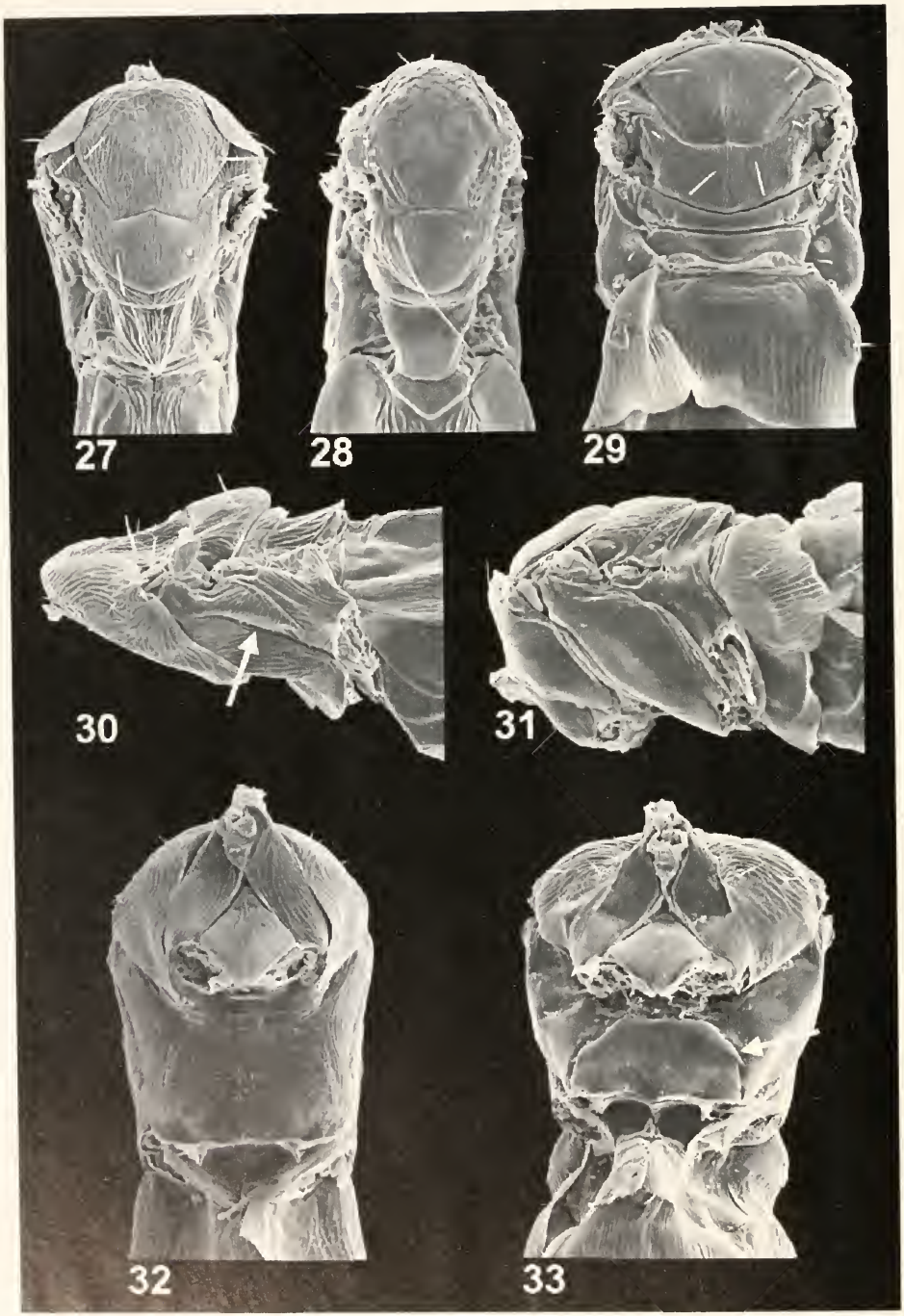
Paroligosita Kurdjumov 1911: 434. Type species: *Paroligosita bella* Kurdjumov, by original designation.

Diagnosis.—Antenna with funicle distinctly separated from 3-segmented club. Maxillary palps present. Fore wing sparsely to moderately densely setose, no more than ca. 4× as long as wide. Propodeal disk not subtended by a small subtriangular lobe.

Antennal structure alone separates *Oligosita* from virtually all other Oligositina. *Megaphragma* and most *Epoligosita* have fewer segments, and *Prestwichia, Prosoligosita* and *Sinepalpigramma* appear to have a 4-segmented club. Any *Epoligosita* with similar antennal structure can be separated by wing and propodeal features. The presence of maxillary palps also separates *Oligosita* from *Sinepalpigramma.*

Comments.—Several species are removed from *Oligosita* and placed in *Pseudoligosita* (see below); approximately 95 species remain assigned. It is likely that further partitioning will be necessary when the group is better known. The lack of clear-cut synapomorphic traits for assemblages other than the Collina Group preclude additional revision at the present time.

Oligosita, as defined here, is readily identifiable but remains paraphyletic and possibly polyphyletic (Fig. 1). For purposes of phylogenetic analysis we divided it into three broad assemblages, as already indicated. The Collina Group (= *Oligosita*-C in Fig. 1), the largest assemblage, almost certainly is monophyletic. In this group, females have a characteristic clavate apical placoid sensillum forming a terminal process on the antennal club (Fig. 19). The group is distinguished further by the structure of the fore wing venation. In most oligositines the premarginal vein does not deviate greatly from the marginal vein but remains close to the anterior margin of the wing. In the Collina Group, the premarginal diverges posteriorly from the marginal vein leaving a distinct costal cell. A further distinction is the placement of the presumed apical premarginal seta in the costal cell rather than on the premarginal vein itself as occurs in most oligositines having two premarginal setae. Most known species of the Collina Group also have a distinctly triangular propodeal disk (Fig. 27).



Figs. 27–33. Mesosoma and base of metasoma. 27–29, dorsal. 27, *Oligosita sanguinea* (Girault) (Collina Group). 28, *Prestwichia*. 29, *Pseudoligosita* (note striate posterior section of metasomal tergum). 30–31, lateral. 30, *Oligosita sanguinea* (arrow to mesopleural suture). 31, *Pseudoligosita*. 32–33, ventral. 32, *Oligosita*. 33, *Pseudoligosita* (arrow to transepisternal sulcus).

The Minima Group (= *Oligosita*-M in Fig. 1) is separated from other *Oligosita* by the arcuate retinacular margin of the fore wing, the single campaniform sensillum at the apex of the premarginal vein and absence of an apical premarginal seta. These traits also occur in other genera of the subtribe and the group may not be monophyletic.

Additional *Oligosita* included here are generalized species which, as a group, do not vary in the characters used for analysis. They were represented in the phylogenetic analysis by a single undescribed species from Western Australia (= *Oligosita*-G in Fig. 1). Their relationship to one another, and to other representatives is unknown. They are retained in *Oligosita* until the genus is better understood.

The Walker type of *O. collina*, the type species, originally from the Haliday Collection, could not be located. It is not deposited in The Natural History Museum (London), The Hope Department of Entomology (Oxford University), or the National Museum of Ireland. Portions of the Haliday collection were widely dispersed to many other museums (O'Connor and Nash 1982) and there is no basis at this time to consider the type lost. We follow the traditional definition of *O. collina* in this paper which defines it as having a clavate sensillum at the apex of the female antenna (Nowicki 1936, Viggiani 1976b) (= Collina Group).

The female types of the type species of *Westwoodella*, *O. subfasciata* Westwood, were examined and are assignable to the Collina Group. The clavate sensillum at the antennal apex, the triangular propodeal disk, and fore wing characteristics clearly place it here. Certain workers (Nowicki 1936, Viggiani 1976b), assuming the absence of the characteristic clavate sensillum in *O. subfasciata*, related the species with an entirely distinct group which we, in part, treat as *Pseudoligosita* (see below). Inconsistencies exist between the types of *O. subfasciata* and the original description of *Westwoodella*. Ashmead (1904) characterizes *Westwoodella* as having a bicarinate metanotum and its funicle as much longer than wide. Neither feature characterizes *O. subfasciata*. The funicle is only slightly longer than wide, and we assume that the 'bicarinate metanotum' refers to the propodeal disk which Westwood (1879) indicates in his drawing of *O. subfasciata* by two subparallel lines.

The types of *Paroligosita bella* are in the Zoological Museum in St. Petersburg. Two of several syntypes were examined. Kurdjumov (1911) considered *P. bella* close to *O. collina* and his description is consistent with certain European species belonging to the Collina Group. The syntypes confirm this.

We examined *Oligosita* from throughout its range. This included over 30 species plus numerous undescribed species. Most species of *Oligosita* parasitize eggs of auchenorrhynchous Hemiptera, particularly Cicadellidae (see Viggiani 1982a, Lin 1994).

Subtribe Eteroligositina Lin, **new status**

Eteroligositini Lin, 1993

Diagnosis.—Antenna with funicle always distinct from club. Fore wings moderately broad, moderately to densely setose; stigma rectangular or subtriangular in shape, usually with a distinct constriction between stigma and marginal vein; mesosoma relatively smooth laterally, obsolescently reticulate dorsally; propodeal disk straplike or only slightly produced posteriorly, not considerably longer than metanotum; pleural suture absent; mesosternum with transepisternal sulci. Metasoma with anterior terga divided into an anterior uniformly sclerotized portion, and a posterior, longitudinally striate section; surface of 1st visible tergum never longitudinally rilled medially. Male genitalia varying in structure.

Comments.—Lin (1993) defined the Eteroligositini to include *Eteroligosita* and *Hay-*

atia based on their distinctive male genitalia. We are returning these genera to the Oligositini but use Lin's family group name as a subtribe.

Based on the examination of several species, any *Oligosita* with longitudinally striate metasomal terga should be transferred to the Eteroligositina. Thus far, we have found that this feature always is correlated with the other mesosomal traits characterizing this subtribe. We are aware of only a single species that remains somewhat questionable as to subtribal assignment. This is *Pseudoligosita gerlingi* (Viggiani). Wing and male genitalic morphology is as in Oligositina. The propodeum, the longitudinally striate metasomal terga, and the relatively smooth mesosomal surfaces place it in Eteroligositina. The two specimens available on slides also suggest the absence of the pleural suture on the mesothoracic segment. This species may represent a basal lineage of Eteroligositina.

Doirania Waterson

Doirania Waterston 1928: 386. Type species: *Doirania leefmansi* Waterson 1928, by original designation. Types examined.

Diagnosis.—Antenna with a single club segment, and a transverse funicular segment. Foramen magnum in a more dorsal position than in other oligositines. Male with a single ventromedial projection on sternum and genitalia similar to that in Oligositina (reduced to a tube with 2 short apodemes at base).

Comments. Doirania was recently reviewed by Pinto (2004). The genus, known from North America, the Palaearctic and New Guinea, currently includes three species. A few species that currently key to *Pseudoligosita* probably belong here. They have a three segmented club, but other features, namely the short, transverse funicle, and dorsal position of the foramen magnum, suggest *Doirania*. Males are unknown. Because of the considerable differences in genitalic structure between *Doirania* and *Pseudoligosita*, generic placement remains questionable. All described species were available for study.

Pseudoligosita Girault

Pseudoligosita Girault 1913: 104. Type species: *Pseudoligosita arnoldi* Girault, by original designation (type examined). **Renewed status.**

Zorontogramma Silvestri 1915: 104. Type species: *Zorontogramma distinctum* Silvestri, by original designation (types examined). Doutt and Viggiani 1968: 537 (as subgenus of *Oligosita*).

Oligosita: Viggiani 1976b: 188 (Arnoldi and Subfasciata groups, in part).

Diagnosis.—Antenna with 2 or 3 club segments; funicular segment usually as long as wide or distinctly longer than wide; linear placoid sensilla normal in width and absent from C1 in species with a 3-segmented club. Fore wing moderately to, rarely, densely setose; setae usually not uniformly distributed on apical half of disk. Hind wing almost always with 2 lines of setae on disk. Ovipositor short to moderately long, rarely surpassing apex of metasoma; third valvula of normal width, never bristlelike. Metasomal venter of male usually with a single elongate, spathulate, sternal projection. Male genitalia of most species with posteriorly directed apodemes at base; genitalia strongly curved ventrally; last sternum not extending beyond apex of last tergum.

The 2–3 segmented club in combination with the relatively short ovipositor (not extending beyond apex of metasoma) separate *Pseudoligosita* from all eteroligositine genera except *Hayatia* and *Eteroligosita*. From these taxa, females are separated by the normal, non-bristlelike, third valvula. Males are easily distinguished by the last metasomal sternum which does not extend beyond the apex of the last tergum.

Comments.—Several species described as *Oligosita* must be transferred to *Pseudoligosita*. Reassignment is based on examination of types or authoritatively identified material and/or clear evidence in-

dicated in the original descriptions. Species referable to *Psudoligosita* (**new combinations**) include the following: *acuticlavata* Lin, *aesopi* Girault, *anima* Girault, *arnoldi* Girault (type species), *brevicilia* Girault, *comosipennis* Girault, *curvata* Lin, *distincta* Silvestri (type species of *Zorontogramma*), *dolichosiphonia* Lin, *elimiae* Viggiani, *elongata* Lin, *fasciata* Viggiani, *fasciatipennis* Girault, *funiculata* Girault, *fuscipennis* Girault, *gerlingi* Viggiani, *gracilior* Novicky, *grandiocella* Lin, *gutenbergi* Girault, *idioceri* Viggiani, *inermiclava* Girault, *krygeri* Girault, *kusaiensis* Doutt, *longiclavata* Viggiani, *longicornis* Lin, *longifrangiata* Viggiani, *lutulenta* Novicky, *marilandia* Girault, *nephotetticum* Mani, *nigripes* Girault, *nowickii* Viggiani, *numiciae* Viggiani, *paphlagonica* Novicky, *plebeia* Perkins, *podolica* Novicky, *phaneropterae* Viggiani, *platyoptera* Lin, *robusta* Viggiani, *schlicki* Kryger, *servadeii* Viggiani, *tachikawai* Yashiro, *transiscutata* Lin, *tumidiclava* Viggiani, *utilis* Kowalski, *xiphidii* Ferrière, *yasumatsui* Viggiani and Subba Rao. Certain species remaining in *Oligosita* probably will require reassignment when studied adequately.

Pseudoligosita probably is paraphyletic (Fig. 1). Its relationship to *Chaetostrichella* and *Probrachista* is unclear but it is possible that the latter two are derived from *Pseudoligosita*. *Pseudoligosita platyoptera* and *P. dolichosiphonia*, two Chinese species, approach *Probrachista*. Both have densely setose fore wings (as in Fig. 6), and *P. dolichosiphonia* also has a strongly exserted ovipositor (see Lin 1994).

Tentatively placed in *Pseudoligosita* are a few species whose males lack metasomal sternal modifications and distinctly curved genitalia (represented in the analysis by *Pseudoligosita*-I but also including *P. gerlingi* and *P. phaneropterae*). Because these species possess features defining the Eteroligositina but none of the generic synapomorphies, they may represent basal subtribal lineages.

The type specimen of *Pseudoligosita arnoldi*, deposited in the Queensland Museum, was examined. Girault (1913) separated *Pseudoligosita* from *Oligosita* by its shorter fore wing fringe, not by any of the features noted here.

Pseudoligosita is cosmopolitan in distribution. Although known to parasitize auchenorrhynchous Hemiptera as do other oligositine genera, several species have been associated with eggs of Orthoptera (Tettigoniidae) and Coleoptera (Chrysomelidae: Hispinae) (see Lin 1993).

Chaetostrichella Girault

Brachystira: Mayr 1904: 590.

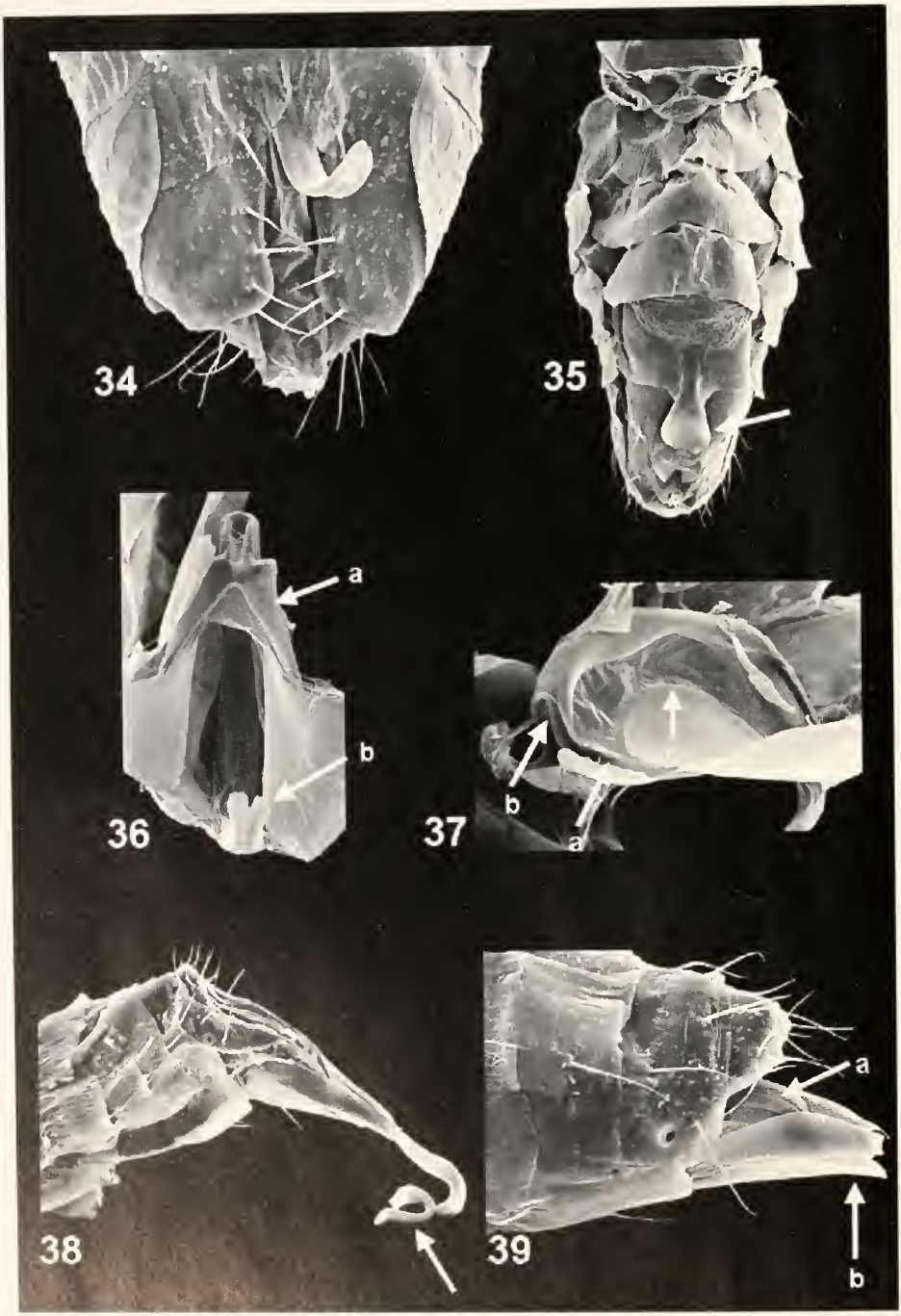
Chaetostrichella Girault 1914: 147. Type species: *Chaetostrichella platoni* Girault, by monotypy. Pinto, 1993: 299 (renewed status).

Brachista: Nowicki 1936: 136. Doutt and Viggiani 1968: 497.

Diagnosis.—As in *Pseudoligosita* except as follows: Antennae with a 1-segmented club (which may be incompletely segmented in some specimens). Fore wing disk beyond level of venation densely, evenly setose; setae not arranged in vein tracks. Hind wing with 2 lines of setae on disk. Ovipositor very long, twice as long or longer than hind tibia, extending well beyond apex of metasoma.

Features separating *Chaetostrichella* from *Pseudoligosita* also separate it from *Doirania*, the other Eteroligositina genus with a single club segment. It also is distinguished from *Doirania* by the elongate funicular segment (transverse in *Doirania*) and male genitalia which, as in *Pseudoligosita*, have 2 strong posteriorly projecting apodemes at the base. The elongate ovipositor and densely setose fore wing also characterize *Probrachista*. However *Chaetostrichella* is easily separated by its 1- segmented club (3-segmented in *Probrachista*).

Comments.—*Chaetostrichella* includes three Palaearctic species (Nowicki 1936, Doutt and Viggiani 1968) which historically were erroneously associated with *Brachista* (see Pinto 1993). It is similar to *Pseudoligosita* and, with *Probrachista*, may represent a derived lineage of that genus.



Figs. 34–39. Male genitalic structures. 34, *Oligosita* (genitalia exserted between divided last sternum). 35, *Pseudoligosita* (venter, arrow to posterior projection of sternum IV). 36, *Pseudoligosita* [ventral, anterior = up; sterna pealed away to expose genitalia; arrow-a to posteriorly directed apodemes at base of genitalia (note anterodorsal aperture immediately anterior), arrow-b to bifid genitalic apex]. 37, *Pseudoligosita* [lateral of genitalia and associated sternal complex; arrow-a to posteriorly directed apodeme which is attached to anterior border of sternum VII; arrow-b to anterodorsal aperture (note ejaculatory duct entering aperture); arrow-c to roof of sternum VII (also see Fig. 14)]. 38, *Hayatia* (lateral, arrow to bifid apex of exserted genitalia). 39, *Hayatia*

Hosts are unknown. Limited collection data suggest that species are associated with aquatic habitats. Our treatment of this genus is based on the study of several unidentified females from Italy and an unidentified male from Kyrgyzstan.

Probrachista Viggiani

Probrachista Viggiani 1968: 521 (in Doutt and Viggiani 1968). Type species *Probrachista nepalensis* Viggiani, by original designation (type examined).

Diagnosis.—Female as in *Chaetostrichella* except as follows: Antenna with a 3-segmented club; 1st club segment loosely associated with C2 and C3, and appearing somewhat as a second funicular segment. Hind wing with 3 complete lines of setae on disk (1 dorsal, 2 ventral). Ovipositor extremely long, greater than twice as long as hind tibia, extending well beyond apex of metasoma; unique for oligositines in that the curved ramus edge of the semicircular sheets are positioned considerably anterior to the gonangulae. Male unknown.

Antennal structure and the 3 setal tracks on the hind wing separates *Probrachista* from *Pseudoligosita*. In addition, the strongly exserted ovipositor, and the evenly, densely setose fore wing disk separates it from virtually all members of that genus (see above for exceptions).

Comments.—*Probrachista* was characterized by Viggiani (1968) as having two funicular and two club segments; the above diagnosis indicates a one-segmented funicle and a three segmented club. Distinguishing between funicle and club segments often is subjective, and this certainly is the case with *Probrachista*. The first club segment is slightly less intimately associated with the second than the latter is with the third. Yet, it is not as distinct from these segments as it is from the funicular segment. For this reason, and so as to not imply a greater difference from other oligositines than is warranted, the club is treated as three segmented.

Only the type species from Nepal is assigned to *Probrachista*. Besides the type series we are aware of two additional specimens (from South Africa and Guinea). Additional material is needed to determine if these are conspecific to one another or to *P. nepalensis*.

As indicated above, *Probrachista* could not be included in the phylogenetic analysis. The overall similarity of females to those of *Chaetostrichella* suggests relationship. Together these genera may represent a derived lineage of *Pseudoligosita*.

Hayatia Viggiani

Hayatia Viggiani 1982b: 27. Type species: *Hayatia indica* Viggiani, by original designation (type examined). Viggiani 1996: 29.

Diagnosis.—Antenna with a single funicular segment and a 3-segmented club. Fore wings moderately broad, ca. 2.5× as long as wide, fringe setae 0.3–0.5 wing width. Hind wing with 3 rows of setae (a central track dorsally and an anterior and posterior track ventrally). Female with 3rd valvula abruptly narrower than 2nd valvifer, bristlelike (see Viggiani 1996). Male with funicular segment shorter than in female; antennal club of male elongate with numerous prominent, linear placoid sensilla on all 3 segments. Metasomal sterna with at least 2 medial prolongations; last sternum of metasoma extending further posteriorly than last tergum. Genitalia extremely elongate, bifid apically, folded on itself when not exserted (see Viggiani 1982b).

Males of *Hyatia* can be confused with no other genus of Oligositini. They are unique in having prominent linear placoid sensilla on all 3 segments of the elongate club. Their unique genitalic structure is shared with *Eteroligosita*. Females of *Hayatia* should be separable from those of *Eteroligosita* by the 3 setal tracks on the hind wing.

Comments.—Five species of *Hayatia* are described from the Ethiopian and Oriental

regions and from Cyprus (Viggiani 1996). The placement of *Paruscanoidea longiclavata* Yousuf and Shafee in *Hayatia* (Yousuf and Shafee 1988) is incorrect. For this study we examined the type species and at least one additional unidentified species.

Hayatia is a close relative of *Eteroligosita* and may eventually prove congeneric. However, because of the considerable difference in male antennal structure we retain generic status.

Eteroligosita Viggiani

Eteroligosita Viggiani 1976a: 265. Type species: *Eteroligosita tamaricis* Viggiani, by original designation (type examined).

Diagnosis.—Similar to *Hayatia* except male antennae without placoid sensilla on first club segment and with enormously enlarged placoid sensilla on the 2nd and 3rd club segment (each ca. ⅔ width of segment). Also, hind wing with only an anterior and middle setal track.

Comments.—The male genitalia in *Eteroligosita* are similar to those in *Hayatia*. The type species was described from Israel; two additional species have been described from China (Lin 1994). *E. tamaricis* was retrieved from galls on *Tamarix* caused by *Amblypalpis olivierella* Ragusa (Gelechiidae). In addition to the type species, we have examined an unidentified species from South Africa (Mooketsi) reared from eggs of *Oxyrhachis rufula* Capener (Membracidae).

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The First Gregarious Species of the Agathidinae (Hymenoptera: Braconidae)

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Abstract.—***Coccygidium gregarium* Sarmiento & Sharkey,** the first known gregarious species of the subfamily Agathidinae (Braconidae), is described. This species was reared from a larva of *Euglyphis* sp. (Lasiocampidae). The SEM images of its last antennal flagellomere reveal that the characteristic acuminate shape is due to the presence of elongated, presumably sensory, structures. This type of flagellomere, together with its carinate hind trochantellus, are traits present in the genera *Coccygidium, Biroia, Dichelosus, Hemichoma* and in the Afrotropical genus *Hyrtanommatium*, suggesting a close phylogenetic relationship. The apex of the ovipositor sheath bears a small pointed process present in other *Coccygidium* species and also in *Biroia, Dichelosus*, and *Hemichoma* but not in *Hyrtanommatium*; this trait may suggest a close relationship among these genera. SEM images of this structure show that it is covered by ampulliform papillae, here reported for the first time. The pores on the inner apex of the ovipositor sheaths and the ampulliform papillae are either secretory or sensory.

The Agathidinae are comprised of approximately 52 genera worldwide, with 20 occurring in the New World. Nearly 1000 species have been described, mostly from tropical areas. The subfamily has been revised at the tribal level by Sharkey (1992), and there have been several faunal treatments and generic revisions (Muesebeck 1927, Marsh 1961, Nixon 1986, Sharkey 1983, 1986, 1988, 1990, Simbolotti and van Achterberg 1999, van Achterberg 1990, and Briceño 2003). The genus *Coccygidium* de Saussure, 1892 (in this paper we follow the generic concept of Chou and Sharkey 1989; including *Zelomorpha* Ashmead) is probably the most species-rich genus of the tribe Disophrini. This genus includes about 35 described species distributed worldwide but more than 100 Neotropical species are awaiting description. Although *Coccygidium* has never been revised, current studies (by C.S. and M.J.S.) suggest that the Neotropical genera *Biroia* Szépligeti, *Hemichoma* Enderlein and *Dichelosus* Szépligeti are derived clades within *Coccygidium*.

All agathidines for which there are reliable rearing records are reported as solitary koinobiont endoparasitoids of lepidopteran larvae. Members of *Bassus* and *Agathis* (Microdini and Agathidini respectively) oviposit in the host, placing the egg inside a ganglion of the ventral nervous system or attaching it to the lateral lobe of the protocerebrum; the larva remains as a first instar, floating in the haemocoel, during the feeding period of the host, and then quickly develops in the final larval and prepupal stage of the host; the final-instar parasitoid emerges after the host has spun its cocoon and completes its feeding externally (Shaw and Huddleston 1991, Sharkey 1997). *Coccygidium* species, as with all the members of the tribe Disophrini, possess short strong ovipositors and parasitize free-living caterpillars in

their late instars. Host records of *Coccygidium* include noctuids, arctiids, notodontids, and lasiocampids (http://janzen.sas.upenn.edu, Shenefelt 1970). Most species of Disophrini are diurnal and brightly colored, but some are nocturnal and have the characteristic pale coloration and enlarged ocelli of nocturnal hymenoptera (Sharkey 1997). In this paper we describe a new species of *Coccygidium* that represents the first record of agathidine larvae living gregariously within a single host individual.

Coccygidium gregarium **n. sp.** Sarmiento & Sharkey

Holotype Female (The variation observed in the paratypes is included in square brackets in italics)

Size. Mesosoma length 2.7 mm (Fig. 1). Forewing length 6.9 mm (Fig. 2).

Color. Mostly black except as follows: basal fourth of fore and mid-tarsi yellow with brown markings; wings infumate; metasoma orange.

Head. Medial ridge or convexity of face present (Fig. 3) [*or absent*]. Face convex medially, flat laterally, lacking striations, with small, sparse punctures laterally, and dense foveolate punctures medially (Fig. 3). Penultimate labial palpomere 25% shorter than apical palpomere. Eyes not emarginate; eyes not converging ventrally (Fig. 3). Posterior orbit not bordered by groove (Fig. 4). Lateral carina of frons incomplete posteriorly, composed of rugae and fovea. Frontal depression smooth. Distance between antennal insertions subequal to their diameter. Number of antennal flagellomeres 35 [*36–37*]. Apical flagellomere acuminate (Figs 5–6). Ratio of distance between inner margins of eyes to distance between lateral margins of lateral ocelli = 1.6. Depression laterad of lateral ocellus absent. Area of vertex posterior to ocelli smooth. Longitudinal depression posterior to ocelli weak, not indicated by distinct groove. Gena, at mid-height, posterior to eye, barely projecting posteriorly rounded, flanged and with a few irregular rugae basad of eye (Fig. 4). Ratio of length of malar space to eye height = 0.3.

Mesosoma. Epicnemial carina complete and with distinct angle. Groove of epicnemial carina wide and flat, with about 10 robust transverse ridges, strongest at mid-length, absent in ventral third (Fig. 9). Mesopleuron uniformly punctured. Precoxal sulcus indicated ventrally by one crenula, otherwise barely depressed and smooth. Posterior margin of mesopleuron with 7–8 robust carinae. Suture between meta episternum and metepimeron complete, smooth, transversed by carinae of subequal size (Fig. 10). Convex flange on posterodorsal border of mesopleuron absent. Dorsal apex of meta episternum with two carinae. Flange at the anteroventral area of metepimeron (i.e., juxtacoxal flange) wide, with a transverse carina (Fig. 10). Area anterior to subpronope not modified into flange or disk. Posterolateral margin of pronotum smooth. Notaulus indicated by weak depression. Median longitudinal mesoscutal groove absent. Scutellar sulcus deep, subquadrate, with 1 [*or 3*] longitudinal carina[e]. Scuto-scutellar articulation absent. Posterior border of mesoscutal sulcus carinate. Scutellum rounded laterally, rugose. Transverse groove of scutellum deep, with crenulae extending anteriorly but not reaching midway to scutellar sulcus. Median areola of metanotum without median longitudinal carinae (Fig. 12). Posterior border of median areola of metanotum acute with acute longitudinal crest. Surface of propodeum with irregular striations (Fig. 12); median, lateral, and pleural areolae present; anteromedial and posteromedial areolae together forming spindle-shaped area with several transverse carinae; anterolateral areola divided by several ridges converging anterolaterally; posteromedial areola with a transverse carina; posteromedial keels weak, converging; transverse keel distinctly curved and complete to pleural carina, dividing pro-

tooth of fore-tarsal claw truncate. Tibial spur of fore-leg 0.58 times as long as basitarsomere. Longest tibial spur of mid-leg 0.68 times as long as basitarsomere. Hind femur rugoso-punctate dorsally and laterally, areolate-rugose ventrally. Longest spur of hind leg 0.53 times as long as basitarsomere. Carina of hind trochantellus weakly indicated (Fig. 11). Apex of hind tibia with 2 or 3 spines arising directly from apical margin. Basal tooth of hind tarsal claw truncate.

Wings. (Fig. 2) 3M vein of fore wing straight. 3RSa vein of fore wing shortly developed. RS2a vein of fore wing longer than r-m cross vein. RS2b vein of forewing absent. CUb vein of hind wing nebulous.

Metasoma. T1 weakly convex. Apex of ovipositor sheath lacking transparent lamella, curved dorsally with a small acute process (Fig. 13). Apex of the ovipositor sheath covered with ampulliform papillae (Figs 14–15).

Male. Does not differ from the female in non-sexual characters.

Etymology: The specific name refers to the gregarious behavior in the larval stage. This is the first known case of gregariousness for the genus *Coccygidium* and for the subfamily Agathidinae.

Distribution: Known from northwestern Costa Rica and from Fortín de las Flores, Veracruz, Mexico, but probably widespread in Central America and southern Mexico. Elevation range: 975–1150 meters.

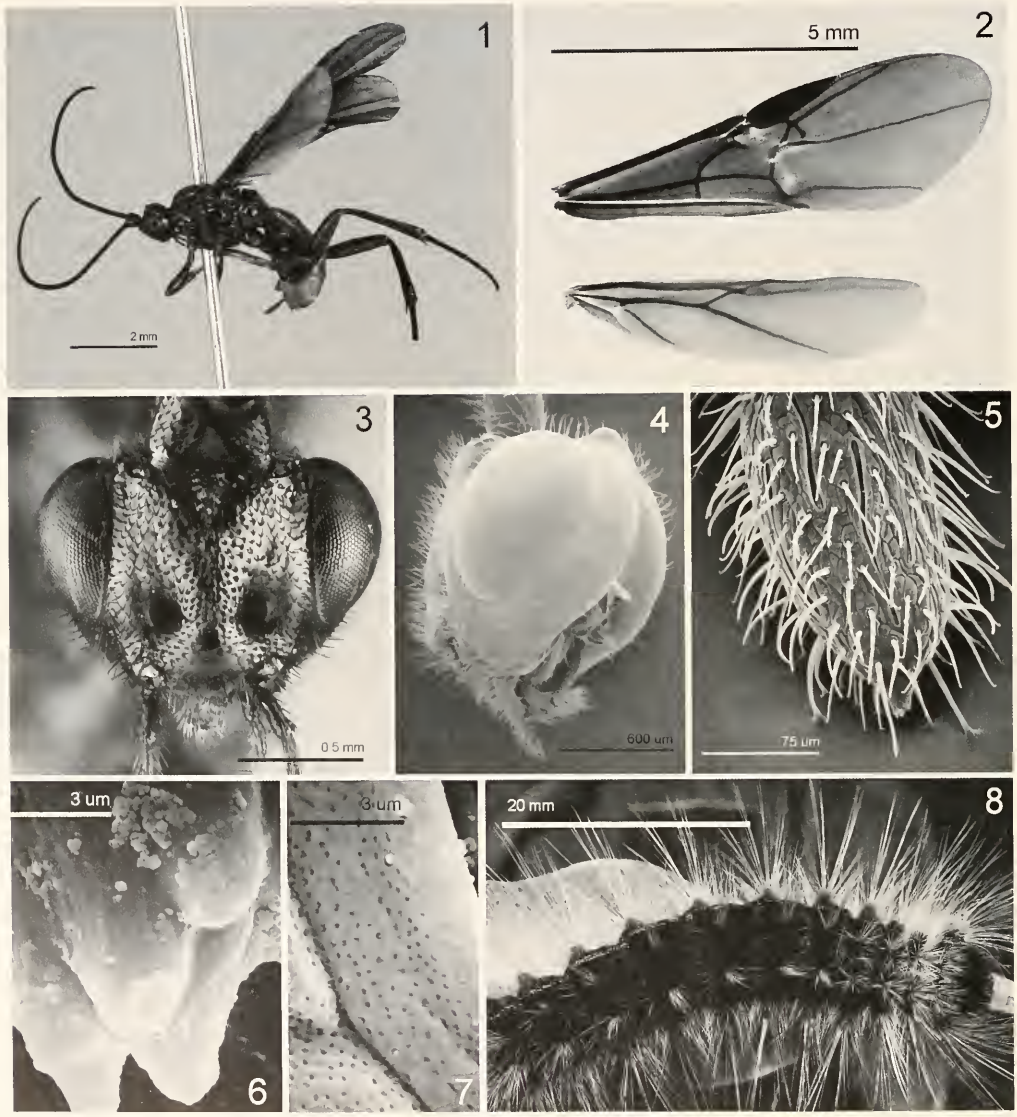
C. gregarium can be distinguished from all other species of the genus by its unique color pattern and by the following combination of morphological characteristics: poorly developed lateral carina of frons; gena at mid-height, posterior to eye, without acute posterior projection; posteroventral area of the gena round and evenly flanged; notauli weakly impressed; propodeum strongly carinate.

Material examined

Holotype female: 1 ♀, (label 1) COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Estación Cacao, 1150 meters, Lambert coordinates: North 323104 East 375725, (Lat 10.92691, Long −85.46822), jul/15/1999, Mariano Pereira collector, voucher 99-SRNP-1161 http://janzen.sas.upenn.edu (label 2) Ex *Euglyphis* sp Janzen14, (Lasiocampidae), feeding on *Beilschmiedia costaricensis* (Lauraceae), (D. Janzen's database 99-SRNP-1161 http://janzen.sas.upenn.edu). Caterpillar prepupal date 3 August 1999, 19 tightly packed, elongate, large, white/gray cocoons completely filling the host cocoon, not silked together. Eclosed on 22 August 1999. Deposited in the Instituto Nacional de Biodiversidad, Costa Rica (INBIO). *Paratypes*: 4 ♂♂, 14 ♀♀, same data as holotype and from same brood; 1 ♀, MEX: Veracruz, Fortín de las Flores, XII-22-63/ Blacklight L. R. O'Brien collector, Insect Collection Los Angeles County Museum of Natural History. Paratypes deposited at INBIO, Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, American Entomological Institute, Hymenoptera Institute, University of Kentucky Insect Collection, and Los Angeles County Museum of Natural History.

Morphology. The acuminate apex of the last antennal flagellomere is composed of six tubular projections (Fig. 5) and, although their shape strongly suggests a sensorial function, high resolution images (Figs. 6) indicate that these processes are devoid of any appreciable sensory structure for chemical reception such as the placoid sensillae or the pores present in other parts of the antenna (Figs. 5, 7). The surface of these tubular projections instead is completely smooth and solid (Fig. 6). These structures may be sensory organs to test physical characteristics such as surface vibrations.

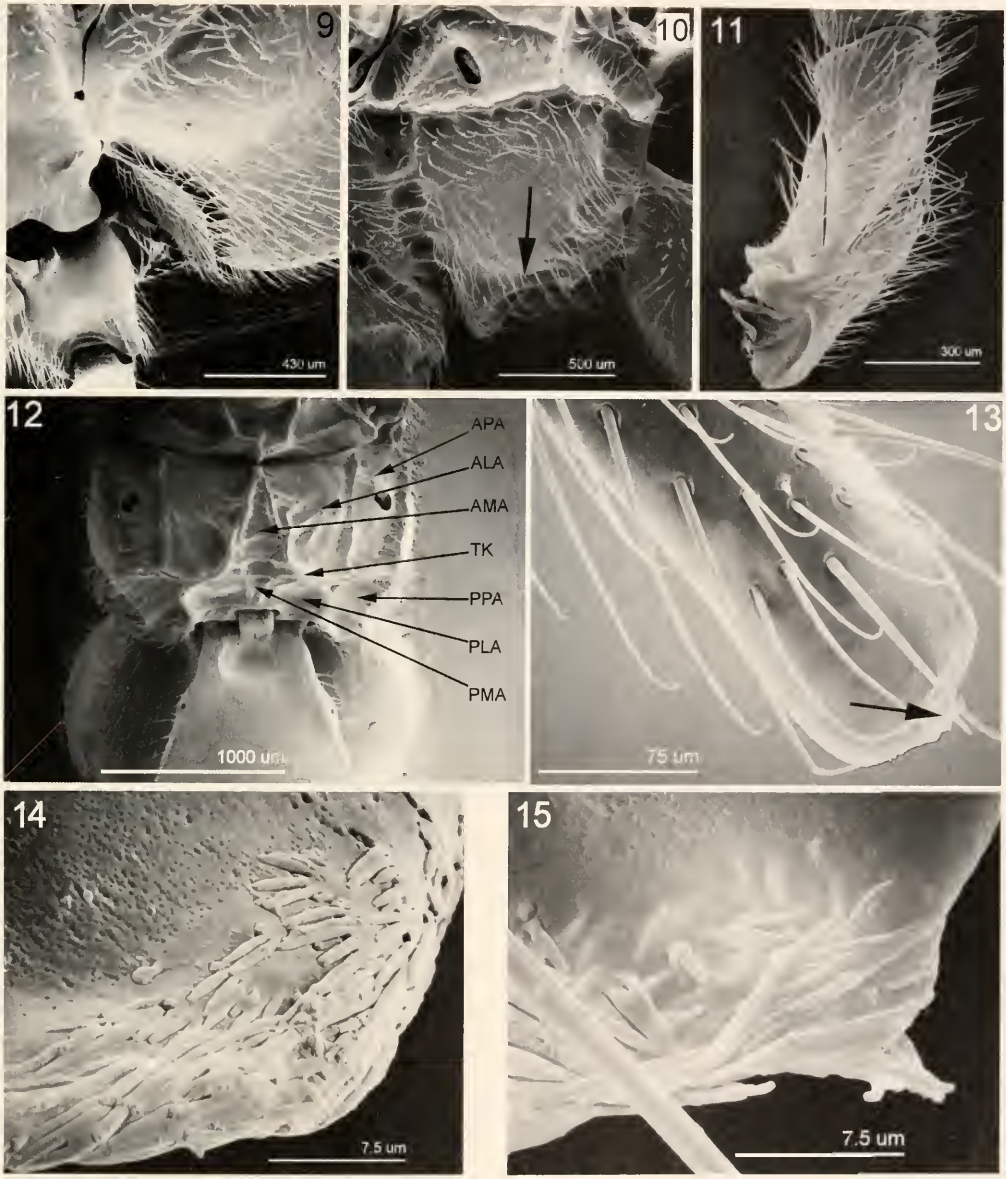
This shape of the last antennal flagellomere is characteristic of all species of the genus, and of the nominal Neotropical genera *Biroia* Szépligeti, *Hemichoma* Enderlein, and *Dichelosus* Szépligeti. We have also observed this trait in the Afrotropical



Figs. 1–8. *Coccygidium gregarium* n. sp.: 1, habitus; 2, wings; 3, head in anterior view; 4, head in lateral view; 5, terminal or last antennal flagellomere; 6, close up of the apex of the last flagellomere; 7, detail of the surface of the antenna far from the apex, note the evenly distributed multiple pores; 8, Habitus of *Euglyphis* Janzen 14, host larva of *C. gregarium* n. sp.

genus *Hyrtanommatium* Enderlein. This character, in conjunction with the carinate hind trochantellus, suggests a monophyletic clade comprised of these genera (Sarmiento & Sharkey, in prep).

The process on the ovipositor sheath is present on most species of *Coccygidium* and in the nominal Neotropical genera listed above, but not in the Afrotropical genus *Hyrtanommatium*. SEM images reveal that this process and most of the sheath apex are covered by ampulliform papillae (Figs. 14–15). In addition, the internal side of the sheath is covered with pores which may indicate the presence of a secretory system. Previous studies have



Figs. 9–15. *Coccygidium gregarium* n. sp.: 9, epicnemial carina; 10, meta-epimeron (the arrow points to the juxtacoxal carina); 11, carina of hind trochantellus; 12, dorsal view of metanotum and propodeum (APA = anteropleural areola, ALA = anterolateral areola, AMA = anteromedial areola, TK = transverse keel, PPA = posteropleural areola, PLA = posterolateral areola, PMA = posteromedial areola); 13, ovipositor sheath (the arrow points to the apical process); 14, apex of ovipositor sheath, medial (internal) view showing the ampulliform papillae (see text); 15, apex of ovipositor sheath, lateral (external) view.

reported the presence of several types of sensory organs on both the ovipositor and the ovipositor sheath of the Hymenoptera (Quicke et al. 1999, Vilhelmsen 2003), but this is the first report of ampulliform papillae. Their function is unknown but possibly they are used to mark hosts with chemical secretions, or they may be sensory structures to test host suitability.

Biology: This is the first gregarious spe-

cies reported for the subfamily Agathidinae. Nineteen adult wasps emerged on 19 August 1999 from a cocoon of *Euglyphis* sp. Janzen14 (Lasiocampidae) (Fig. 8). The lasiocampid cocoon was filled with 19 elongate tightly packed large white/gray silk cocoons that were, however, not silked, glued, or otherwise attached to each other. The wasp larvae emerged from the prepupa of the host as is typical for all known species of Agathidinae. The lepidopteran larva (Fig. 8, and also images at http://janzen.sas.upenn.edu, voucher code 99-SRNP-1161) was collected as a penultimate instar on 15 July 1999, and spun on 3 August 1999, in the full rainy season. Its food plant, *Beilschmiedia costaricensis* Mez & Pittier, is among the many lauraceous trees fed on by at least 10 species of *Euglyphis* Huebner in this rainforest—cloud forest intergrade located on the western slope of Volcán Cacao, Area de Conservación Guanacaste (ACG), northwestern Costa Rica. The two localities where specimens of *C. gregarium* have been collected, Estación Cacao and Fortín de las Flores (Mexico), are extremely similar in their climate and in their original vegetation/ecosystem (personal observation, D.H.J.), despite being respectively on the Pacific and Atlantic coasts of Central America and being separated by several thousand kilometers.

Through 2002, the 24-year-old ongoing lepidopteran larvae inventory of the ACG (e.g., Burns and Janzen 2001, Janzen 2003, Janzen et al. 1998, 2003, Schauff and Janzen 2001, Sharkey and Janzen 1995) has reared 1,452 wild-caught lasiocampid larvae, 98% of which are members of 20+ species of *Euglyphis*, without any other rearings of *C. gregarium*. Indeed, these larvae only produced 21 other hymenopterous parasitoids, all of which are representatives of a single undescribed species of Microgastrinae (*Parapanteles* "par22", Braconidae, det. Alejandro Valerio). Since this species of *Euglyphis* (Janzen14) has not been found either previously or subsequently by the inventory, it is either a very rare species or one that normally lives in the crowns of tall trees. These traits may apply to *Coccygidium gregarium* as well.

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Notes on the Biology of *Lycorina triangulifera* Holmgren (Hymenoptera: Ichneumonidae: Lycorininae)

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Abstract.—Host searching behaviour, oviposition and the ovarian egg of the koinobiont ichneumonid *Lycorina triangulifera* are described. Oviposition attacks were observed on two species of leaf spinning tortricid larvae, the ovipositor being inserted into the host's anus. The ovarian egg does not have the sinuous and leech-like characteristics described and figured by Iwata (1958). Rather, its elongate oval shape is unremarkable, but it carries a small anchoring device at its (presumed) caudal end. This strongly suggests that the egg is laid externally with respect to the host cuticle. One adult was reared from the experimental tortricid host *Acleris schalleriana*, but observations were not close enough to ascertain whether the development of the larva was endoparasitic or ectoparasitic. Nevertheless, it seems probable that *Lycorina* is essentially a koinobiont ectoparasitoid with an unusual egg placement.

This paper presents an opportunistic study on aspects of the biology of an ichneumonid, *Lycorina triangulifera* Holmgren, belonging to a small subfamily, Lycorininae, whose systematic position within the Ichneumonidae remains uncertain. Direct observations on the biology of the Lycorininae have not previously been published (but see Coronado-Rivera et al. 2004).

The subfamily is widely distributed in the world but according to Yu and Horstmann (1997) it contains fewer than 30 valid described species, all classified in the genus *Lycorina* Holmgren, although Townes (1970) had recognised three closely related genera in the subfamily (*Lycorina*, *Gonioglyphus* Seyrig and *Toxophoroides* Viereck), each distributed in a different part of the world. Although some credible rearing records exist (from various "microlepidoptera," traceable via Yu & Horstmann 1997), no details beyond that of the host's name have been published (but see also Coronado-Rivera et al. 2004). One species, *L. triangulifera*, occurs widely in the Palaearctic region and has very occasionally been collected in southern England in wooded habitats. It has been widely recorded as reared from Tortricidae, Yponomeutidae, Pyralidae and Gelechiidae. Unfortunately the relatively large number of literature citations of these hosts generally fail to make it clear whether the record given is a reiteration of a previous (but unreferenced) citation, or a new finding: none that I have seen is detailed or authoritative enough to be worth citing here, but references to arboreal Tortricidae seem the most diverse and therefore perhaps the most credible. There is also a welter of references to the cerambycid beetle *Saperda populnea* (Linneaus) as host, but again they may all relate to a single supposed occasion which is in any case likely to have been erroneous. Gauld (1997) briefly discusses the host records of other species, emphasising Pyralidae and Tortricidae, but Lycorininae remains one of the few subfamilies of Ichneumonidae for which practically nothing is known about its developmental biology (but see Coronado-Rivera et al. 2004).

Cushman & Rohwer (1920) first proposed independent status for Lycorininae on the basis of its morphological isolation.

and succeeding authors (e.g. Perkins 1959, Townes 1970) have maintained that view. More recently, molecular phylogenies (D. L. J. Quicke et al. pers. comm.) have continued to emphasise its distinctiveness. According to D. L. J. Quicke (pers. comm.) the D2 region of the 28S rDNA gene is on a long branch: in parsimony analyses with all other subfamilies *Lycorina* tends to associate either with Anomaloninae or with Hybrizontinae; however, members of both also exhibit long branches, and therefore such placements are best regarded as artefactual. The detail of the ovipositor structure, in which the upper valve is divided in two with a separate piece linking them, is similar to that seen in some of the possibly basal "ophioniformes" (e.g. Stilbopinae, Cremastinae, Banchinae, Phytodietini, Idiogrammatini and some Phrudinae), suggesting another possible affinity (Quicke et al. 1994, Quicke pers. comm.), although single sections of such structures are difficult to interpret with confidence. Further information illustrating the uncertain phylogenetic position of Lycorininae is summarised by Coronado-Rivera et al. (2004).

MATERIALS AND METHODS

In view of its previously known distribution in Britain, it was a great surprise when, at about 23.30 BST on 29.vi.2003, a female specimen of *L. triangulifera* came to a 160w MV-Tungsten blended light over a sheet run (with a generator) at Wood of Brae, on the Black Isle (Cromarty), in N. E. Scotland (Grid Ref. NH 692628). The habitat consisted of a ca 10m strip of boggy heath between a vehicle track (with open heathland on the other side) and birch-dominated thicket woodland, with stunted (browsed) bushes of *Betula*, *Alnus* and *Salix* near to the light. It is not an unusual habitat in Scotland, though the presence of several species of orchid and other ground flora suggested that it had been moderately stable. The female was kept alive, fed *ad libitum* on 1:3 honey:water, pure honey and pure water (all of which were accepted, sparingly, at different times) in the 7.5 × 2.5cm corked glass tubes in which she was always kept and offered potential hosts. The simplest aim was to try to discover its oviposition biology, but unfortunately most of this necessarily happened during a holiday in Belgium and E. France (8–26.vii.2003), when the frequent travelling as well as sometimes high temperatures made it difficult to keep the female in good condition (and may have hastened her death on 24.vii.2003). It was also difficult to make as many or as detailed observations as would have been desirable, and neither suitable photographic nor microscopy equipment was to hand. Further, only wild-collected hosts were available to offer to the female, and the supply of these was sparing. Possibly parasitised hosts were reared singly in 7.5 × 2.5cm corked glass tubes, with absorbent tissue paper pressed into the bottom (cf. Shaw 1997). For most of the period until 26.vii.2003 they were under essentially indoor conditions, but subsequently all livestock was kept in a fully shaded and well ventilated outdoor shed.

A further female, collected in France: Dordogne, St Alvère, by Malaise trap 13–25.vi.2002 (*R.R.Askew*) was stored in ca 60% ethanol until 15.ii.2004, when its ovarian eggs were examined by dissection.

All adults of *Lycorina triangulifera* mentioned in this work are deposited in the National Museums of Scotland.

RESULTS AND DISCUSSION

Host Acceptance Trials

In early trials (2–6.vii.2003) the general behaviour of the female *L. triangulifera* towards Lepidoptera larvae and their faeces was found to be as follows: naked hosts (both "macro" and "microlepidoptera") were never of the slightest interest; faecal pellets, if small, offered alone often elicit-

Table 1. Responses of adult *Lycorina triangulifera* (1 ♀) to various "microlepidoptera" larvae in leaf spinnings. (No ovipositions occurred).

Larva	Instar	Leaf spinning	Faeces attractive?	Probing?
Agonopterix sp. (Oecophoridae)	Final	*Angelica*	No	No
Diurnea fagella (Dennis & Schiffermüller) (Oecophoridae)	Early	*Fagus*	—	Yes
2 × *Hypatima rhomboidella* (Linnaeus) (Gelechiidae)*	Final	*Betula*	No	No
Ancylis uitterbacheriana (Dennis & Schiffermüller) (Tortricidae)	Penultimate	*Quercus*	—	Yes
Indet. (Tortricidae)	Penultimate	*Crataegus*	Yes	Yes
Indet. (Tortricidae)	Penultimate	*Rosa*	Yes	No
Indet. (Tortricidae)	Final	*Salix*	No	No
Udea sp. (Pyralidae)	Final	*Rubus*	Yes	No
Indet., absent	—	*Acer*	—	Yes**
Indet., absent	—	*Salix*	—	Yes**

* Both turned out to be already parasitised by *Meteorus pulchricornis* (Wesmael) (Braconidae).
** Vacated roll probed for more than 3 minutes.

ed intense antennation and simultaneous (or closely subsequent) probing with the ovipositor, a little forward of vertically, against the glass of the tube (faeces of young Geometridae and Notodontidae feeding on *Betula* were the most attractive tested, but comparisons were few); leaf spinnings containing "microlepidoptera" larvae often elicited probing responses. The faecal pellets of larval sawflies (Hymenoptera) in the families Argidae (on *Salix*) and Tenthredinidae (on *Betula* and *Spiraea*) were as unattractive as the larvae that produced them. Various wild-collected "microlepidoptera" larvae concealed in leaf spinnings were offered *in situ* in the period 2–23.vii.2003 but not parasitised, although in some cases they elicited probing responses. The results of these trials, which mostly involved single examples of the Lepidoptera species, are expressed in Table 1. Many of these larvae were already in their final instars when offered and, in view of later experiments, it seems possible that at least some may have been too far advanced to be acceptable.

The remainder of the observations (in the period 12–23.vii.2003) were made on tortricid species into which ovipositions apparently occurred (*Ancylis apicella* (Dennis & Schiffermüller) (Olethreutinae) in *Frangula alnus* Miller and *Acleris schalleriana* (Linnaeus) (Tortricinae) in *Viburnum opulus* Linnaeus spinnings); potential hosts that could be collected in small numbers where my wife and I were holidaying, allowing at least a bit of continuity and control. Although three apparent ovipositions were observed in *A. apicella* (and a further three larvae may have been oviposited into, as each had to be left unobserved while the parasitoid was probing its leaf roll) only adult moths resulted from all exposed hosts (all but one completed their development in 2003 rather than entering diapause as a fully fed larva). In contrast, the only *A. schalleriana* into which oviposition took place resulted in progeny. No difference was seen in the way the female *Lycorina triangulifera* behaved towards these two tortricids, which both seemed fully acceptable to her despite the apparent difference in developmental success. The following descriptions of probing and oviposition behaviour are based on these hosts. The host individuals concerned were all associated with single spun leaves, in which they were well established. Some of the *Ancylis apicella* larvae offered were well grown in their final

instar but most (and all *Acleris schalleriana*) were in earlier (second to penultimate) instars, and ovipositions were only seen in hosts within that range.

Probing Behaviour

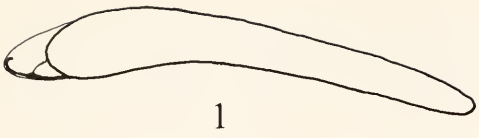
Leaf rolls (or folds—"roll" is used to cover both) were rapidly accepted and climbed onto following very brief antennation. Probing with the ovipositor followed immediately, interspersed with much antennation of the substrate. The ovipositor was rapidly and repeatedly plunged deeply into the roll, showing no favour for windowed or holed areas; the female made these successive insertions as she moved along the roll, giving the impression that she was following detected movements of the host. This impression was enhanced by her repeated, sudden and rapid turns (often 180°) and subsequent methodical probings along a new line. However, some of the rolls she investigated were sufficiently windowed for the (unchanging) position of the host larvae to be seen, and other rolls in fact contained no larvae, so these sudden changes of tack in the parasitoid's searching appear to be completely independent of host behaviour, and at least the initial contact with the host seemed therefore to depend largely on chance. Although the parasitoid's probing appeared to be extremely meticulous and thorough, on several occasions she was observed to spend more than 20 minutes continuously probing a roll but failing to contact the host within. Rolls in which this happened were eventually abandoned, at least for a time, after about 25 minutes. The vigour with which she plunged the ovipositor through intact leaf tissue, with no apparent hesitation for site selection, and the number of times she seemed to have to do it in order to parasitize a single host, may go some way towards explaining the very robust and toothed ovipositor tip of *Lycorina* and also the relatively large subgenital plate (hypopygium) that supports its shaft. The strongly pectinate claws would presumably provide the grip needed to accomplish such sudden turns. The high time investment that appeared to be necessary to parasitise a host is surprising in view of the rather high number of ovarian eggs noted by Coronado-Rivera et al. (2004), and may suggest that females live for quite a long time.

Oviposition Behaviour

Altogether five successful contacts with a host larva were seen, in which it appears the host was extremely rapidly injected with a venom as contact was made, resulting in a temporary and only partial loss of movement. In one case the host immediately wriggled completely out of the end of the roll unnoticed by the parasitoid and was not rediscovered in its subsequent torpor, but in the other four what looked like successful subsequent ovipositions were seen.

In two cases the host (one each of *Ancylis apicella* and *Acleris schalleriana*) wriggled head first out of the roll before becoming subdued, and was rapidly grabbed by the parasitoid which held it in her front and middle pairs of legs (orientated head to head) while the ovipositor tip was inserted carefully into the host's anus, and held there for ca 2–2.5 minutes. The ovipositor was then withdrawn, the host released, and the adult parasitoid left the scene. Within a few minutes the host had recovered full mobility and re-entered its roll. There was no discernible difference in the parasitoid's behaviour in these two cases and, although only one of the hosts (*A. schalleriana*) subsequently produced a parasitoid, an egg appeared to have been laid in both cases.

The other two presumed ovipositions (into *A. apicella*) took place through the leaf tissue with the host larva still inside the roll, and in only one case could the host be seen clearly enough for the site of oviposition to be established: again into the anus. In one case the host larva half-



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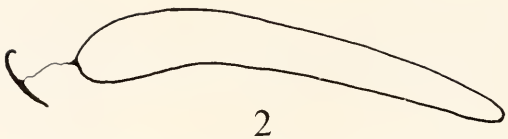

2

Figs 1–2. Mature ovarian egg of *Lycorina triangulifera*. 1. As it appears in the oviduct. 2. Freed from the apparently membranous tissue seen in Fig. 1.

emerged head first from the roll but was driven back inside by the parasitoid (using its front legs and possibly antennae to hit the larva), and in the other the larva became subdued without exposing itself. The apparent ovipositions took ca 1.5 and ca 2.5 minutes. Although only a proportion of ovipositions appear to involve grasping the host, the strongly pectinate claws of *Lycorina* may also help it to do this.

The Ovarian Egg and Subsequent Development

Iwata (1958) described and figured the ovarian egg of *Lycorina triangulifera* as sinuous and leech-like, completely unlike that of any other known group of Ichneumonidae. Iwata's work does not make clear how the *Lycorina* egg was obtained or prepared, but this peculiarity of the egg of *Lycorina* has been widely cited and is an important part of the enigma surrounding its biology.

The female specimen of *L. triangulifera* from France which was preserved in ca 60% ethanol for about 20 months was in a slightly distended condition when it was dissected. The elongate, white, densely packed ovarian eggs measured 0.62 mm in length and were apparently in good condition. Projecting from the side of the broad leading end (presumably the caudal end: cf. Quicke 1997) of each was a fine brown linear structure, aligned with the long axis of the egg and enclosed in what appeared to be a weak membrane (Fig. 1). When freed from this, the linear structure could be seen to be a thin sclerotised bar, sharply curved at one end (the end that projects in Fig. 1), and attached from its midlength to a protuberance at the extreme end of the egg by a fine flexible strand (Fig. 2). Coronado-Rivera et al. (2004) have independently discovered and described closely similar devices on the eggs of two species of *Lycorina* from Costa Rica.

Egg placement via the host's anus might in principle be either subcutaneous (i.e. internal) or external with respect to the body of the host, as the lining of the hind gut of caterpillars is part of their cuticular tissue (and sloughed with the rest of the cuticle at ecdysis). At least two other species of Ichneumonidae are known to oviposit into their host's anus. One, *Chorinaeus funebris* (Gravenhorst) (Metopiinae), oviposits into the hind gut and the ensuing larva crosses the gut wall to become an endoparasitoid for the rest of its development (Aeschlimann 1974). In the other case, *Eromenus calcator* (Müller) (Tryphoninae), the egg is fastened to the inside wall of the hind gut and larval development is ectoparasitic throughout (Zinnert 1969). With its very clear anchoring device, it seems probable that the egg of *Lycorina* is positioned externally to the body of the host, albeit in a concealed site, and that *Lycornia* may be essentially an ectoparasitoid. However, until definitive observations can be undertaken the more remote possibility that oviposition is subcutaneous cannot be completely ruled out.

Unfortunately the progress of experimental hosts could not be followed closely enough to provide clear evidence for the site of larval development. The single experimental host (*Acleris schalleriana*) from

which a parasitoid was reared was parasitised (as a probably early third instar larva) on 20.vii.2003, and became prepupal about 8.viii.2003, soon after which its cocoon was opened and the prepupa briefly inspected (but from one side only), without anything unusual being noted. The host cocoon was opened again on 14.viii.2003, by which time the *Lycorina* larva had become fully fed, pushed the host's prepupal cuticular remains entirely to one end of the host's cocoon, and spun its own translucent, very fine and frail membranous cocoon—indistinguishable to me from that typical of *Glypta* (Ichneumonidae: Banchinae) species—in the space that had been occupied by the host prepupa. A slightly deformed female *Lycorina triangulifera* emerged on 6.ix.2003, having chewed a rough hole through the side of the cocoon near its apex and also the adjoining dry leaf tissue. It was fed *ad libitum* on 1:3 honey:water and kept under outdoor shade conditions of daylight and temperature, but its behaviour did not suggest that it would attempt to hibernate and it died on 1.x.2003.

While the above observations demonstrate that *Lycorina* is a koinobiont killing the host as a prepupa, unfortunately they are not complete enough to ascertain how the larva develops. As noted by Coronado-Rivera et al. (2004), the final instar larva has some characters usually seen in endoparasitoids, but also denticulate mandibles (Finlayson 1976, Short 1978, Chao 1980) like those of several groups of ectoparasitic Ichneumonoidea but unlike those of fully endoparasitic ones, suggesting that *Lycorina* may develop as an ectoparasitoid, at least in its final feeding phase. This, indeed, has been confirmed by Coronado-Rivera et al. (2004). Although a switch from endophagy to ectophagy is known to occur widely in non-cyclostome Braconidae (Shaw and Huddleston 1991), in Ichneumonidae it has been believed to occur only in the Eucerotinae (Tripp 1961), whose biology is remarkable for its extreme specialisations (though in fact actual development during the parasitoid's internal phase has not been clearly demonstrated for Eucerotinae). Thus it would be surprising if a genuine switch from endophagy to ectophagy occurred in Lycorininae, and a more parsimonious conclusion would be that, in the strict sense of not being subcutaneous, it is probably an external parasitoid throughout, however long it may take for the larva to emerge from the host's anus. It is frustrating in the extreme that the interventions made were ill-timed to elucidate this crucial aspect of its biology.

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Does Temperature Affect Diploid Male Production in *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae)?

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Abstract.—As in many other hymenopterans, sex in *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) is determined by single-locus complementary sex determination. Thus, unfertilized eggs become haploid males and fertilized eggs that are homozygous and heterozygous at the sex locus develop into diploid males and females, respectively. We investigated the effect of temperature during development on the production and survivorship of diploid males. Females were allowed to oviposit at 20°C and 27°C and progeny remained at the same temperature throughout development. Diploid males were produced at both temperature regimes indicating that temperature does not affect sex determination in *H. hebetor*. However, temperature did affect diploid male survivorship, which was higher at the low temperature.

In haplo-diploid hymenopterans, sex is usually determined at oviposition with fertilized eggs developing as females and unfertilized eggs developing as males (Cook 2002). Haplo-diploidy is achieved in many hymenopterans by a mode of sex determination known as single-locus complementary sex determination (Whiting 1943, Cook 1993, Cook & Crozier 1995, Butcher et al. 2000a, b, Beukeboom 2001). In this system, sex is determined at a single genetic locus with multiple alleles. Sex-locus heterozygotes develop as females and sex-locus homozygotes develop as diploid males. Haploid males (hemizygotes) are produced from unfertilized eggs as in standard haplo-diploidy. Diploid males are inviable or sterile and females that mate with diploid males produce all male (haploid) offspring or, rarely, sterile triploid females (Bostian 1936, Stouthamer et al. 1992, Cook & Crozier 1995, Holloway et al. 1999).

As it is currently understood, complementary sex determination (CSD) is a form of genotypic sex determination in which sex is determined at fertilization and does not change over the course of the organism's life. Genotypic sex determination can be contrasted with sex determination mediated by cytoplasmic factors (Stouthamer et al. 2002) and with environmental sex determination, in which sex is determined by environmental factors such as temperature (Cook 2002). Temperature-dependent sex determination is quite common in reptiles and some other vertebrates (Bull 1983) and there is evidence for a mixture of genotypic and temperature-dependent sex determination in some of these species (Kraak & Pen 2002).

Investigations of temperature-dependent sex determination in insects are rare, but an early study on CSD in the parasitoid *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) reported a decreased incidence of diploid males in the offspring of females that were held and allowed to oviposit at 20°C rather than at 30°C (Whiting & Anderson 1932). Whiting and An-

derson's study suggested the possibility of an important link between temperature and sex determination (i.e., sex-allele homozygotes developing as females at low temperatures), but their results could also have been explained by decreased survivorship of diploid males at the lower temperature. Also, the time period during which sex determination would have occurred was poorly defined in their study since females and their offspring were held at the different temperatures for several days prior to, and following oviposition. Three more recent studies have also suggested that sex determination may be dependent upon temperature in parasitoids, and in all of these cases the critical sex determination stage was identified as the egg or early larval stage. Butcher et al. (1996, 1998) reported that *Diadegma chrysostictos* (Gmelin) (Hymenoptera: Ichneumonidae) and the sexual strain of *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) produced diploid males only when reared from the egg or early larval stage at temperatures exceeding 22°C, although Beukeboom (2001) could not repeat these results with *V. canescens*. An additional study reported that *H. hebetor* females allowed to oviposit at low temperature produced few or no diploid males despite intense inbreeding (Butcher 1998, personal communication). This result is consistent with the earlier findings of Whiting and Anderson (1932) but the critical time for sex determination was identified as being the egg or early larva. Here, we revisit Butcher's findings on temperature-dependent sex determination in *H. hebetor* by investigating the effects of developmental temperature on diploid male production and survival.

MATERIALS AND METHODS

Background on *H. hebetor*

Habrobracon hebetor is a gregarious ectoparasitoid of several species of phycitine pyralid moths (Heimpel et al. 1997). Females inject paralyzing venom into their hosts and lay three to twenty eggs on the surface of the host (Benson 1973). In the laboratory, *H. hebetor* females usually fertilize about two thirds of their eggs resulting in the production of a female-biased secondary sex ratio by outcrossed females (Petters & Mettus 1980, Antolin & Strand 1992, Heimpel et al. 1997, Ode et al. 1997). However, under CSD, the secondary sex ratio is altered when males and females share a sex allele since half of the fertilized eggs develop into diploid males. In *H. hebetor*, between 90 and 95% of diploid males typically die in the egg stage (Heimpel et al. 1999). Thus, females mated to males sharing a sex allele produce broods that are reduced in size by approximately one third and that have an even or slightly male-biased secondary sex ratio (Petters & Mettus 1980, Heimpel et al. 1999). Extreme polymorphism at the sex locus (Whiting 1943, Heimpel et al. 1999) and outcrossing (Antolin & Strand 1992, Ode et al. 1995) make the production of diploid males rare in the field (Antolin et al. 2003). However, conditions of inbreeding and restricted genetic diversity can lead to the production of diploid males (Whiting 1943, Heimpel et al. 1999).

Experimental *H. hebetor* were obtained from a colony reared on *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae) larvae in an environmental chamber at the University of Minnesota at 25° C, 75% RH, and 16:8 photocycle (L:D). Two strains of *H. hebetor* were used. One strain carried a recessive eye color mutant exhibiting pale green eyes. This strain dates back to early work on *H. hebetor* done by P.W. Whiting and associates (see Whiting 1961) and retains the label "Oi". The second strain is a wild-type (black eye) strain collected in Kobe, Japan. Both strains were kept as separate 2-allele isolines initiated by mother-son matings and continued by brother-sister matings (see Heimpel et al. 1999). To avoid any confounding effects of *Wolbachia*, which is commonly present in

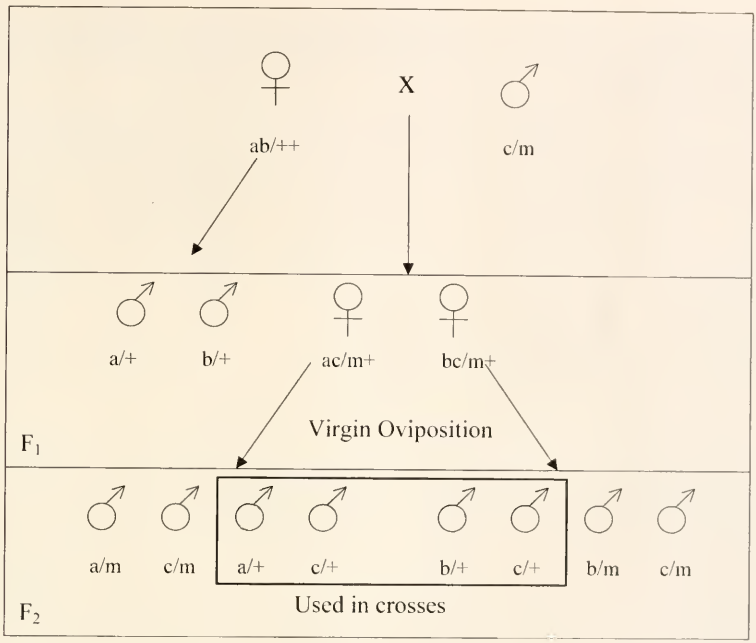

Fig. 1. Crosses showing production of recombinant males. Parents are from two unrelated isolines and presumed not to share any sex alleles. Sex alleles (a–c) and eye color (+ = wild type, black; m = mutant type, green) are indicated below each individual. The allele 'c' is used as a designator for one of two alleles present in the mutant line that differ from both of the alleles in the wild-type line. Virgin oviposition of F_1 females resulted in only recombinant male progeny, half of which were black-eyed. Black-eyed males were then mated with mutant females from the original parental mutant isoline, which carry the 'c' sex allele.

H. hebetor (M.F.A., L.A.W. & G.E.H. unpublished), we used the progeny from a cured isoline that were fed 10mg/ml rifampicin in 10% honey for 72 hours. The absence of *Wolbachia* was confirmed before and after the experiment by using a primer pair for a section of the *Wolbachia* wsp gene (Zhou et al. 1998). In these amplifications, uncured *H. hebetor* used as controls exhibited the expected 590 to 632-bp product (Zhou et al. 1998), and the offspring of cured *H. hebetor* showed no product. *Plodia interpunctella* were reared on a diet of wheat bran, chick feed, corn meal, glycerol, honey, and water (ca 43:30:14:9:2:2 by volume) at 25° C, 75% RH, and a 16:8 photocycle.

Experimental Crosses

Crosses were designed to ensure matings among males and females sharing a sex allele (henceforth referred to as 'matched' matings) and eye color markers were used to distinguish diploid from haploid males. First, recombinant *H. hebetor* males were produced from matings between wild type and mutant adults (Fig. 1). These recombinant males were then mated with virgin females from the maternal mutant isoline. One-half of the fertilized offspring of these shared-allele matings will be diploid males, recognizable by paternal inheritance of the wild-type eye color (black). Haploid males, which develop from unfertilized eggs, retain the maternal mutant eye color (green).

Each of twenty mated females were given two *P. interpunctella* for oviposition and a drop of honey each day until their death. Females were allowed to oviposit at 20° C for 2 consecutive days and then transferred to 27° C to oviposit for one day before returning to 20° C. We gave *H. hebetor* two days to oviposit at the cool tempera-

Table 1. Means (± S.E.M.) of the numbers of eggs laid per *H. hebetor* female, the egg hatch rate, the overall developmental mortality, the proportion of adult offspring that were females, and estimates of the fertilization rate and diploid male survivorship.

	Matched matings (n = 10)		Unmatched matings (n = 10)	
	20°C	27°C	20°C	27°C
Eggs laid/female	134.6 ± 6.14	134 ± 8.98	127.3 ± 9.26	104.7 ± 14.66
Egg hatch rate	0.78 ± 0.02	0.76 ± 0.02	0.91 ± 0.02	0.88 ± 0.02
Dev. Mortality	0.39 ± 0.03	0.38 ± 0.04	0.15 ± 0.03	0.14 ± 0.03
Secondary sex ratio (Proportion female)	0.39 ± 0.05	0.38 ± 0.05	0.60 ± 0.03	0.58 ± 0.06
Fertilization rate	0.57 ± 0.06	0.55 ± 0.06	0.60 ± 0.03	0.58 ± 0.06
Diploid male survival	0.6 ± 0.01	0.02 ± 0.01	N/A	N/A

ture because the oviposition rate is lower at 20° C than at 27° C. When females were transferred to another temperature, hosts were not provided until females had acclimatized to the new temperature (ca 2 hours). Eggs produced by mothers were transferred daily to freshly paralyzed, egg-free *P. interpunctella* using a blunt probe. Eggs and *P. interpunctella* were kept in 35 × 10 mm plastic petri dishes (Sarstedt Series #83.1800). Three eggs were placed on the ventral side of each paralyzed *P. interpunctella*, one near the head, one between the first and second pairs of prolegs, and one near the posterior, and were checked daily for hatching. Egg to adult development took place in an environmental chamber at 20° or 27° C, 75% RH, and a 16:8 L:D photocycle.

Data Analysis

Data recorded included the number of eggs laid and the egg hatch rate, larval—adult developmental success, and the sex and eye color of eclosing adults. Each mating was classified as "matched" if any diploid males were produced, and "unmatched" if no diploid males were produced. All black-eyed males were identified as diploids. Fertilization rate was estimated differently for matched ((total females × 2)/((total females × 2) + total haploid males)) and unmatched matings (number of females/total adult progeny). Diploid male survivorship was estimated as (diploid males/females) on a per-family basis. Data were analyzed using matched pairs analysis with each female serving as its own control (SAS Institute 1995). Two females produced all male progeny and were excluded from analyses as it was assumed that they had not mated.

RESULTS

Temperature during development did not affect production of diploid males by *H. hebetor*. We found evidence for single-locus CSD at both 20° C and 27° C, with patterns for both temperatures very similar to previous studies (Whiting 1943, Petters & Mettus 1980, Heimpel et al. 1999). Table 1 summarizes the mean ± SEM egg hatch rate, overall developmental mortality, sex ratio, fertilization rate, diploid male survival rate, and total eggs laid per female *H. hebetor* for matched and unmatched matings at 20° and 27° C. The average number of eggs laid ranged between 105 and 135 per female with significantly fewer eggs laid by females from unmatched matings at 27°C (interaction between temperature and mating type: $P < 0.05$). The egg hatch rate was not significantly affected by temperature, but was significantly lower when eggs were laid by females of a matched mating ($P < 0.001$). Similarly, developmental mortality was significantly higher in the matched matings ($P < 0.001$) but not significantly

affected by temperature. The estimated fertilization rates were not significantly affected by temperature or mating type, but sex ratios were significantly more male-biased in the matched matings ($P < 0.01$), as expected when most diploid males die during development. Finally, the estimated diploid male survival rate was significantly higher at 20° C than at 27° C ($P = 0.05$).

DISCUSSION

Our results are not consistent with Butcher's finding of a lack of CSD when development occurs at low temperatures (Butcher 1998, Butcher et al. 1996, 1998). Instead, our findings suggest that the developmental temperature has no effect on sex determination mode. What could account for this difference? One possibility is that our negative results are an artifact of our *H. hebetor* being *Wolbachia*-free. We have recently screened two wild populations of *H. hebetor* for *Wolbachia* and found both to be infected (M.F.A., L.A.W., G.E.H. unpublished). It is therefore possible that the stocks of *H. hebetor* used by Whiting & Anderson (1932) and Butcher were infected with *Wolbachia.* If temperature-dependent sex determination is only expressed by *Wolbachia*-infected *H. hebetor,* then our lack of a temperature effect could be attributed to the absence of *Wolbachia.* However, a separate study in which temperature effects on CSD were evaluated in *Wolbachia*-infected *H. hebetor* yielded results similar to the ones reported here (Weiser et al., in preparation).

Our failure to find temperature-dependent CSD parallels Beukeboom's (2001) failure to find temperature effects on CSD in a sexual strain of *V. canescens,* which had originally been reported by Butcher et al. (1998). In both of these cases, the potential for intraspecific variation in sex determination and related traits cannot be excluded. It is becoming clear that sex determination mode is evolutionarily flexible and that relatively closely related taxa can have different forms of sex determination (Werren & Beukeboom 1998, Kraak & Pen 2002, Cook 2002). In some animals, variation in the sex determination mode has even been found among populations of the same species. Examples of non-symbiont-related intraspecific variation in sex determination include a fish, the woodlouse *Armadillidium vulgare,* a shrimp and the housefly, *Musca domestica* (reviewed by Werren & Beukeboom 1998 and Cook 2002). Sex determination has not been reported to differ within species in Hymenoptera, but it is clear that some species of braconids have sl-CSD while other species do not (Beukeboom et al. 2000, Wu et al. 2003) and this level of variation appears to be present within a single braconid genus as well. CSD has been identified in *Cotesia rubecula* (Stouthamer et al. 1992 and personal communication of W.W.M. Steiner to L.A.W.), but not *C. flavipes* (Niyibigira 2003). Determining whether there is variation among hymenopteran strains in sex determination mode or diploid male survivorship will have to await side-by-side studies of strains that are reported to be temperature-sensitive and temperature-insensitive.

Although the reasons for the difference between our results and those of Butcher (1998) remain unclear, it is still conceivable that the temperature that females experience prior to oviposition has an effect on sex determination. Whiting and Anderson (1932) reported a lower incidence of diploid males from females that were both held and allowed to oviposit at 20°C rather than 30°C. Because Whiting and Anderson did not report data on fecundity, egg hatch, or developmental survivorship, it is not clear whether these differences are due to true differences in sex determination (i.e., sex allele homozygotes developing as females) or to differences in the survivorship of diploid males. For this reason, and because Butcher (1998) had identified the egg or early larva as the critical stage for sex determination, we did

not test for an effect of the temperature experienced by females on sex determination. Thus, our experiment is not a repeat of Whiting and Anderson's (1932) work and leaves open the possibility that the temperature female *H. hebetor* experience prior to oviposition affects sex determination.

While all species of *Habrobracon* studied to date have exhibited sl-CSD, the survivorship of diploid males varies greatly among species (Speicher & Speicher 1940, Clark et al. 1963, Holloway et al. 1999) and within *H. hebetor* (Whiting & Anderson 1932; Petters & Mettus 1980; this study). In our study, diploid male survivorship was significantly higher at the low temperature. Temperature-dependent survivorship rates of diploid males can have important implications for the population-level effects of CSD in the field. Viable diploid males that are sterile yet that participate in mating have stronger (negative) effects on population sizes than inviable diploid males, because females mated to these sterile diploid males are constrained to producing only haploid sons (Stouthamer et al. 1992; Holloway et al. 1999). Our finding suggests that these dynamics may be linked to temperature fluctuations in the field.

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NOTE

A Replacement Name for the Cleptoparasitic Bee Genus *Rhathymodes* (Hymenoptera: Apidae)

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We recently proposed a new genus for two species of cleptoparasitic bees in the tribe Rhathymini (Apidae: Apinae). Unfortunately, the name we employed is preoccupied in the Lepidoptera; it does not appear in Neave's *Nomenclator Zoologicus*. We, therefore propose the following replacement name to correct this nomenclatorial difficulty:

Nanorhathymus Engel, Michener, and Rightmyer, new name

Rhathymodes Engel, Michener, and Rightmyer 2004: 6. Type species: *Rhathymus acutiventris* Friese 1906, original designation. *Nomen praeoccupatum* [*nec Rhathymodes* Turner 1911 (Lepidoptera: Lasiocampidae; today considered a junior subjective synonym of *Opsirhina*)].

Etymology.—The new genus-group name is a combination of *nanos* (Gr., meaning "small") and *Rhathymus*, type genus of the tribe, and is a reference to the smaller body size of these species. The name is masculine.

Included species.—The genus includes, *Nanorhathymus acutiventris* (Friese), **new combination,** and *N. bertonii* (Schrottky), **new combination.**

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Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used (if any), including discussion of program options used. A data matrix should be provided if the subject is complex. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and reasons given for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For multiple authors, use the word "and," not the symbol "&" (Smith and Jones 1999). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

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All manuscripts and correspondence should be addressed to:

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Biological Records Centre

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